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The genus Pandanus in the Mascarene Islands.

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(With Plates **1–4**, 3 Text-figures and 1 Map)

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INTRODUCTION

The family Pandanaceae comprises three genera: *Sararanga* with two species confined to the Philippines, New Guinea, and the Solomon Islands; *Freycinetia* with over 200 species extending from Ceylon through Indonesia to the Pacific and southwards to Australia; and *Pandanus*, the most widely distributed of the three genera, with probably over 350 species spread through Tropical Africa, Madagascar, the Mascarenes, to Tropical Asia, Indonesia, and the Australo-Pacific Region. The three genera thus occupy concentric areas with *Sararanga* in the middle surrounded by *Freycinetia* which in turn is embraced by *Pandanus*.

Some nineteenth-century systematists considered the family to be one of the most primitive of the monocotyledons, and in the system adopted by Engler and Prantl in the *Pflanzenfamilien* the Pandanales, with the Sparganiales and Typhales, are placed in the first or lowest series of monocotyledons with very simple flowers without bracts or perianth. Modern ideas (Hutchinson, 1934) incline to the view that the Pandanaceae are an advanced group, much reduced, derived from the Agavaceae and closely related to the palms. It is not possible here to enter into a detailed review of the possible phytogenetical connexions of the family, though it may be that the facts revealed by a study of the Mascarene species may throw some light on these problems.

ETYMOLOGY

The screw-pines or pandans are known in the Mascarene Islands as *Vacoas*, the spelling of which occurs in numerous variants such as *Vakoa*, *Vaquois*, *Baquois*, *Vacoua*, *Vaqoua*, and so on; in Rodriguez they are called *Vacoa poteau*, *Vacoa parasol*, *Vacoa Chevron*, *gros Vacoa* according to the habit of the species. In Madagascar, a variety of names are used, the particular name indicating some characteristic feature or the purpose for which the plant is employed; thus we have *Vakoana* for the large-leaved forms used in making fibre and mats, *Satrana* species with small leaves, and *Fandrana* very tall forms with slender leaves.

In Réunion the word *Baquois*, derived from an old French word *Baquier* meaning 'a coarse cotton from Smyrna', was formerly common. Could we not then conclude that the present-day names for screw-pines in this region are derived from the French *Baquier*, a word brought to Madagascar and the Mascarenes by the early French settlers?

A different answer to this question is suggested, however, when we turn to Flacourt's *Histoire de Madagascar* (1661). Here we find that the name *Vakoa* was already in use before any French words could have been absorbed into the Malagasy language. Further, Flacourt refers to the screw-pines as *Pendre*, a French corruption of the Malagasy word *Fandrana*. But *Fandrana* or *Fandrane* (the last syllable being mute in Malgache) is surely derived from pan-dan, the common Malay word for screw-pines which have scented flowers or foliage. It is probable, therefore, that the word *Vakoa* also has a Malay origin. When screw-pines are used for making mats the Malays call them *menkuwang* or *bengkuwang*; eliminating the *ng* in the first and last syllables gives *bekuwa* from which it is a short step to *vekuwa* or *vakoa*, the *O* in Malgache being pronounced as *U*.

The Malagasy names for screw-pines and their Mascarene derivatives thus afford another example of the well-known close affinities between the Malagasy and the Malayo-Polynesian group of languages, though, as hundreds of years have elapsed since the first wave of Malayan invaders reached Madagascar, considerable alteration and divergence in many words must be expected.

Historical Retrospect

The genus *Pandanus* has a difficult and complicated botanical history, of which a brief summary may be given here. The earliest record of *Pandanus* appears to be in Acosta's *Tractado de las Drogas* (1578) in which a crude drawing of a pandan is found over the inscription *Ananas bravo*; later, John Bauhin (1651), in his *Historia Plantarum*, reproduces the same cut but changes the name to *A. sylvestris*. In the classical folios on the botany of the East by Rheede (Hortus Malabaricus) and Rumphius (Herbarium Amboinense) more than a dozen species are figured and described, and the Malay name *Pandang* is used by the latter.

The superficial resemblance of the pandan syncarp to a pineapple seemed to have impressed early writers, and J. Burman (1737), in his *Thesaurus Zeylanicus*, groups the pandans then known under the name of *A. sylvestris* which was changed to *Bromelia sylvestris* by Linnaeus (1747) in his *Flora Zeylanica*. The distinctive character of the genus was not understood until the material collected during the voyage of H.M.S. *Endeavour* to the South Seas was examined.

An extensive collection of pandans was made by Charles Gaudichaud-Beaupré during his voyage round the world in the *Bonite*, and many of his specimens were figured in his sumptuous Atlas which appeared in 1841–52; unfortunately, no contemporary descriptions were published and the exact locality of much of his material is open to doubt. The great variety shown in the shape and arrangement of the drupes and stigmas led Gaudichaud to split the genus into a large number of smaller genera; but Balfour (1878), who published a synoptic list of the genus, discarded the smaller genera of Gaudichaud and other authors and retained *Pandanus* for the whole group. This treatment was followed by Warburg (1900) who monographed the family for Engler's *Pflanzenreich*. Warburg gave brief descriptions of over 150 species, and divided the genus into ten sections which he named for the most part after the smaller genera of Gaudichaud, his sections being based mainly on the nature of the stigmas and the arrangement of the drupes.

The untimely death of Dr Ugolino Martelli has delayed the publication of the comprehensive monograph of the genus on which he had been engaged for many years; he had, however, already published an illustrated Enumeration of nearly 300 species with a geographical conspectus (1913–14) and an important paper on the distribution of the family (1933); he had also described a number of new species including two from the Mascarene Islands.[1] Botanical exploration in the Far East and the Pacific Islands during recent decades has brought to light many new species which have been described by Kanehira and others, and it may be safely assumed that the genus comprises over 350 species.

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[1] This paper was ready for the press when an important monograph by Martelli and Pichi-Sermolli (1951) was published on the species of *Pandanus* collected by Perrier de la Bathie in Madagascar. The paper describes four new sections and thirty-eight new species, one of which most probably belongs to the section *Keura*.

Turning to the Mascarene region we find that among the earliest descriptions of the pandans is that of Francois Leguat (1708), who, in his *Voyages et Aventures*, has left us the following curious account of the Rodriguez species:

> Among the great number and variety of Trees in this Island planted by Nature, there is one which is wonderful and worthy our particular Observation, for its Beauty, Bigness, Roundness, and the rare Symmetry of its exact Branches; the ends of which are every where much tufted, and its Leaves so great and thick, that they fall down almost to the Ground all about it; so that come which way you will at this Tree, you can perceive but a small part of its Trunk, and that at the bottom of it; and sometimes you can see nothing at all of it.
>
> It being as one may imagine, all shady in the middle, the Branches are within-side like dry Poles, which seem to be the work of a Carpenter, and set there to bear up the Plumes or Branches which are quite about it, and thus make a sort of Cage or Tent of the Tree. 'Tis true, the greatest beauty of this Tent, is in its charming Outside, though the coolness and shelter of the inside have also their Charm; 'twas unhappy that its Fruit was not good to eat. Those of us who had the Curiosity to eat it, found it Sour, and knew by Experience, that was all the hurt that was in it. It has the smell of a very fine Quince; 'tis a sort of a Grape, the Seeds of which are close and all together. It lookt at a distance like the Fruit of Ananas. For which reason we us'd to call these Trees Ananas; tho' there's a great difference between the two Plants. As for me, I was for calling it the Pavillon or Tent.

With the exception of Leguat only very brief references to Mascarene pandans are found in early Dutch and French writers of the period, no doubt because the great majority of the species occur in the then inaccessible marshes and stream banks of the interior. Our knowledge of the genus may be said to date from the beginning of the nineteenth century when Bory de St Vincent (1804) visited Réunion and described three species from there, and A. du Petit Thouars (1808) botanized in Madagascar and the Mascarenes and published the first account of Mascarene pandans recording sixteen species of which six were from Mauritius. Captain Dugald Carmichael, of the 73rd Regiment, was collecting plants in Mauritius and Réunion between the years 1812 and 1814, and prepared an illustrated description of the pandans which was never published; his manuscript is preserved in the library of the Linnean Society.

The observations of Bory and Du Petit Thouars, supplemented later by the collections of Gaudichaud, formed the basis of the lists and descriptions of Mascarene pandans prepared by various authors during the next sixty years, including Lamarck (1810), Sprengel (1826), Kunth (1841), Steudel (1841), Voigt (1845), Kurz (1867), and Brongniart (1875). In his *Hortus Mauritianus* (1837), Bojer also recorded the species of Bory and Thouars, and, in addition, listed some cultivated forms the identity of which it is now almost impossible to establish.

The next step in our knowledge of the local screw-pines was the result of searches made by John Horne, Director of the Botanic Gardens of Pamplemousses, and Sir Henry Barkly, Governor of Mauritius from 1863 to 1870. During the 1870's we find Horne busily collecting specimens for Kew, and he was awarded a special grant of £20 for this purpose. Studying the voluminous letters and notes he sent to Kew at this period it is interesting to read his remarks in a letter to the Director, then Sir William Thistleton-Dyer: 'I really do not know when all the species and varieties of Pandanus in Mauritius will be sent to you. Localities hitherto unvisited are frequently productive of new forms and it is likely that more remain to be discovered in some other parts of the island'—a prediction which has indeed proved to be correct. The material collected by Barkly and Horne was used by Balfour for his synopsis of the genus referred to above and for the descriptions of the screw-pines which he wrote for Baker's *Flora of Mauritius and the Seychelles* (1877). Balfour (1879) visited Rodriguez with the transit of Venus Expedition and described the pandans of the island in his *Botany of Rodriguez*. Cordemoy (1895), in his *Flore de l'Ile de la Réunion*, though not adding to the species already noted by previous authors, gives useful observations on the habit and distribution of the species endemic in the island.

WORLD DISTRIBUTION

Like an enormous truncated triangle with its apex in West Africa, the distribution area of *Pandanus* stretches across Tropical Africa and the lands bordering the Indian Ocean and expands into a vast area in the Pacific ranging from the Bonins and Hawaii in the north to the Tubai Islands south of Capricorn. The general features concerning the distribution of the genus as a whole are now fairly clear and may be summarized as follows:

(i) Distribution is typically insular with only sparse or sporadic occurrence on the continental masses.

(ii) Endemism is extremely marked, each island supporting its own characteristic species.

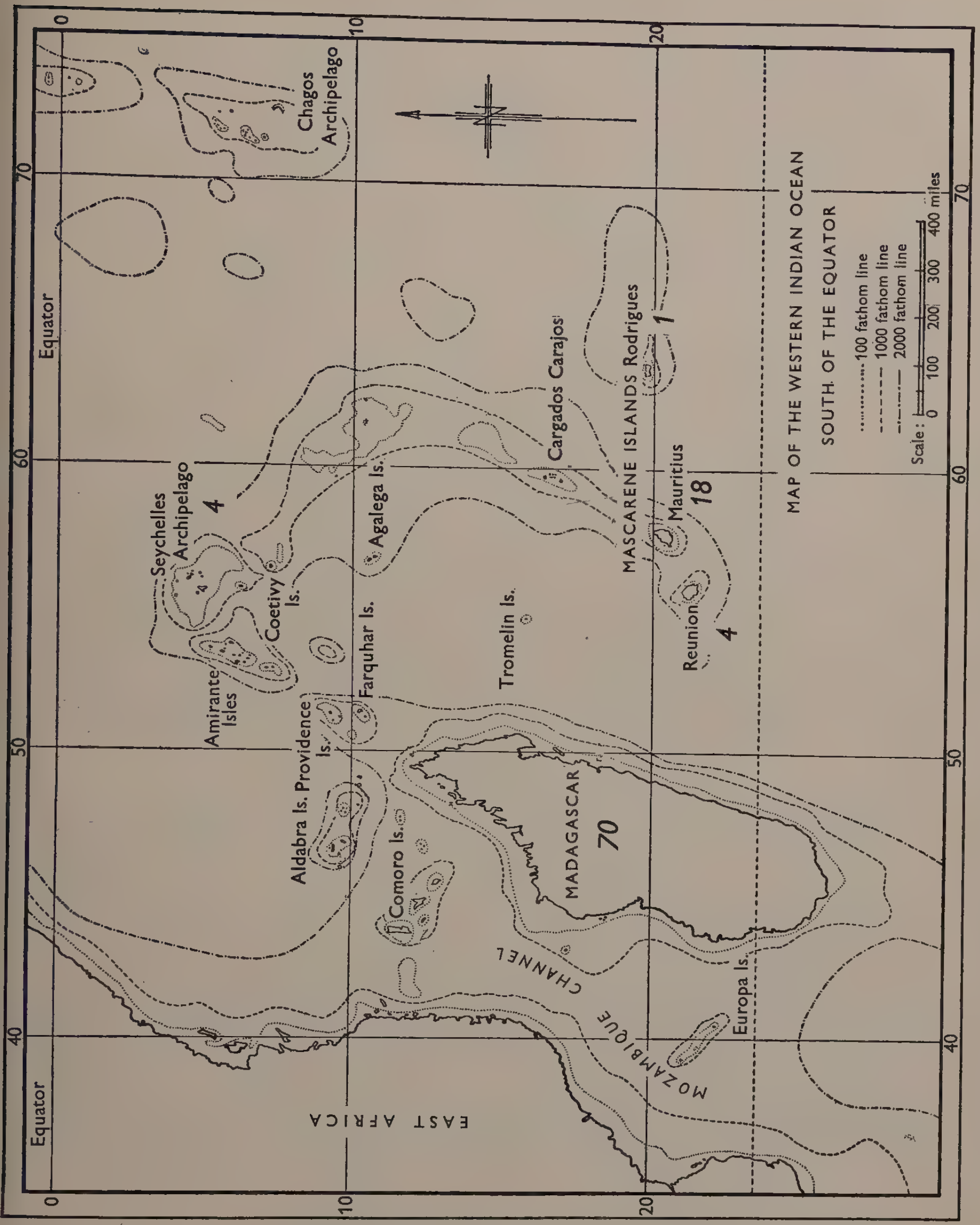
(iii) The species reach a maximum concentration in two focal areas, one in the islands of the south-west Indian Ocean, the other in Indonesia.

The distribution of the pandans in the islands of the south-west Indian Ocean is shown in the map, from which it will be seen that this region well illustrates the characteristic type of distribution shown by the genus. The number of species in Madagascar is about 60–70, much exceeding those on the African continent, and in Mauritius, with an area of only 720 square miles, 15–18 species occur, a remarkable concentration of pandans far exceeding that in any other part of the Afro-Malagasy region, and only paralleled by the Micronesian Islands (Kanehira, 1935), from where over 65 species have been described by Martelli and Kanehira.

Coming now to the distribution of the sections into which the genus is divided by Warburg and Martelli, we find that the section *Keura*, which contains the largest number of species, including the very variable and widely cultivated *P. tectorius*, has an extremely wide distribution ranging from Micronesia to Mauritius (*P. palustris*) and the Seychelles (*P. sechellarum*) and with possible representatives in East Africa and Madagascar. Though there may be reasons to support Martelli's view that the African species of this section have been introduced by man, there can be little doubt concerning the endemic character of the Mauritius species *P. palustris*. The section *Keura* is thus of great interest, forming as it does a link between the western and eastern zones of the genus. A further link between the two regions is provided by the occurrence in Madagascar of certain species which, judging from the structure of the fruits, appear to belong to the Indo-Pacific sections *Rykia*. Apart from the species mentioned above, the Mascarene species belong to the Afro-Malagasy sections *Vinsonia* and *Sussea*. The distribution of these sections in this region is further discussed under phylogeny.

ECOLOGY IN MAURITIUS

In Mauritius, it is in the uplands under conditions of high rainfall that the screw-pines attain their maximum development and concentration of species. Two regions in particular call for comment: first, the Fressanges-Midlands marshlands at an altitude of 450 metres occupying an area of roughly 250 hectares with a mean annual rainfall exceeding 5000 mm.; and secondly, part of the south-western plateau where the altitude reaches 650–725 metres and the mean annual rainfall varies from 3000 to 3800 mm.; this region has an area of about 750 hectares. In the former area *Ravenala* is making serious inroads into the pandan marshes, but the Les Mares-Le Pétrin district of the south-western plateau is still a veritable pandanetum in which are crowded a dozen or more endemic species occupying various stages of the sere. Many sites in the uplands, formerly rich in pandans, have either been built over or converted into reservoirs, and at the present time the screw-pines are practically confined to the marshy areas described above, and to the banks of the upper reaches of the streams which debouch from them.



Map. Distribution of *Pandanus* in the islands of the Western Indian Ocean south of the equator. The numbers, which are only approximate, indicate the species in the different islands or archipelagos; the figure for Madagascar includes the Comores. No indigenous species is common to two or more islands.

The ecology of the pandan marshes in the uplands has already been briefly discussed in a previous paper reviewing the plant communities as a whole (Vaughan & Wiehe, 1937). Under water-logged conditions *P. palustris* (Pl. **1**, fig. D) is frequent, usually growing in streams and pushing up numerous pneumatophores, while a dense mass of stilt roots grows down from the trunk, some even emerging from beneath the terminal crown of leaves (Vaughan & Wiehe, 1931, Pl. **11**, phots. 1, 2, p. 305). Other species thrive in the peculiar soil conditions produced in the marshes, where a thick grey subsoil has been formed practically devoid of iron; here the pandans grow in dense consocies forming gregarious thickets dying away in the centre and spreading out into the surrounding bogs. The upper branches of these marsh-loving pandans often become top-heavy and collapse by their own weight, or are broken off by cyclones and continue to grow on the ground by means of adventitious roots. In the interior of these thickets drier soil conditions are produced favouring the growth of small, more mesophytic phanerophytes and ferns; these marsh-loving pandans include *P. sphaeroideus*, *P. rigidifolius*, *P. barklyi*, *P. carmichaelii*, *P. prostratus* and *P. glaucocephalus*. It is noteworthy that several species are able to thrive under a wide range of edaphic conditions experiencing at the same time such a striking change in their life-form and physiognomy as to make it difficult to identify them by their vegetative characters. Thus some of the species noted above may be found also in the highly xerophytic *Philippia-Helichrysum* scrub growing on the unweathered slab-like lava which often very abruptly succeeds the marshes. A characteristic species occurring in rocky soil or on the border of marshes is *P. drupaceus* (Pl. **1**, fig. A). One species, *P. eydouxia* (Pl. **1**, fig. F), is able to penetrate as far as the *Sideroxylon* thicket which is the sub-climax to the upland climax forest; unlike the marsh and scrubland species which have a semi-decumbent thicket-forming habit, *P. eydouxia* gives rise to scattered clumps of five to fifteen individuals with stout erect boles often exceeding 10–15 metres high and over-topping the low canopy formed by the dominant species of *Sideroxylon*. Several species, including *P. microcarpus*, occur on the banks of upland streams, particularly where periodical flooding has retarded the development of the climax forest.

Only one species is littoral, *P. vandermeerschii*, but it is not associated with mangroves, preferring rocky or exposed cliffs and beaches; it is found on most of the islets bordering the mainland and is common on Round Island growing with endemic palms (Pl. **1**, fig. E). Other species may have existed in the lowlands, though the remnants of drupes recently found with dodo bones in the coastal marshes at Mare aux Songes and Mare aux Mulets appear to belong to the existing species *P. vandermeerschii* and *P. utilis*.

The Mascarene pandans have not taken kindly to the advances of civilization. The draining and reclamation of marshes and scrub-lands, competition by exotics, and the depredations of monkeys and man have all taken a heavy toll; some species are already extinct while others are bound to become so in a few years. Attempts are being made to establish local screw-pines in the Botanic Gardens at Pamplemousses and part of the natural pandanetum near Les Mares is to become a National Reserve; by these means it may be possible to preserve for posterity some of the ancient remnants of the Mascarene flora.

FLORAL DEVELOPMENT AND GERMINATION

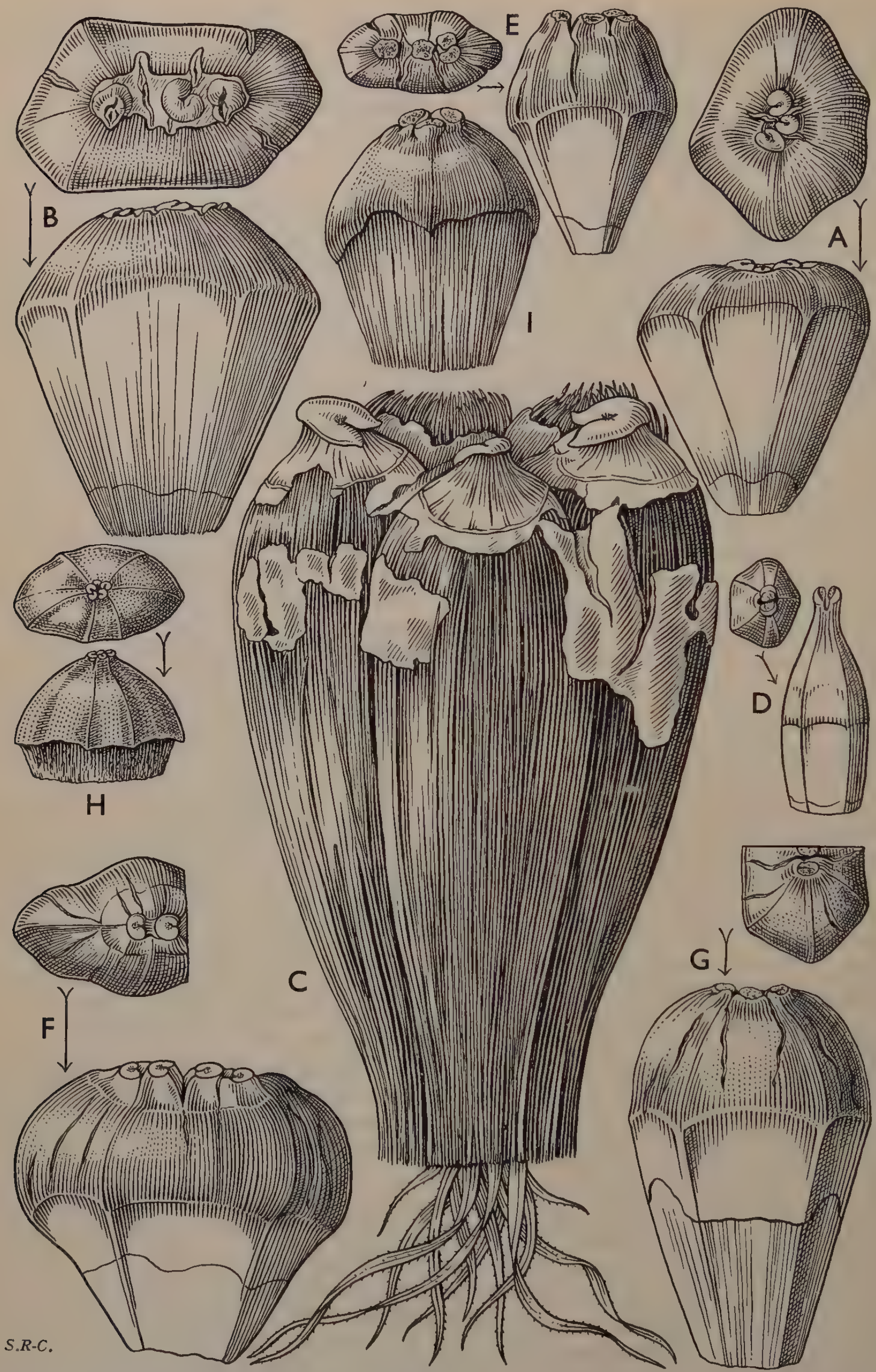
Although anatomical and morphological studies have been made by several workers on a few species, mostly cultivated in botanic gardens, our knowledge of the life history of the screw-pines remains extremely meagre. In so far as the Mascarene species are concerned we know practically nothing of the germination, reproductive capacity, viability of the seeds, early development, onset and periodicity of flowering, distribution of the sexes and many other important questions fundamental to a proper understanding and appreciation of the genus. Taxonomic studies have also presented much difficulty owing to the lack of adequate herbarium material and to the scanty knowledge we have of the plants in the field. Up to the present, the monographs written on the genus have been based mainly on herbarium collections of drupes which show great variation according to the position in which they occur on the syncarp and the age of the latter when they are gathered. The present study is the outcome of field work extending over a number of years, individual plants having been kept under observation in most cases, and the following notes gleaned during the course of collecting material for this paper may be of interest.

The early stages of both the male and female flowers may usually be found in November or December before the onset of the summer rains, and their formation can usually be detected by a slight bulge in the centre of the terminal crown of leaves. In some species the female head remains swathed by large leaf-like bracts with only a small portion of the syncarp visible. In others the female 'flower' is enclosed by contorted fleshy, white, or pink-tinged bracts which fall apart exposing the creamy foetid-smelling stigmatic surface of the future syncarp; this type of flower is quite striking and has a beauty not usually associated with screw-pines (Pl. 4, figs. E, H). The syncarp at this stage is about 2–3 cm. diameter and borne at the end of a stout fleshy peduncle which exhibits a remarkably rapid elongation after fertilization.

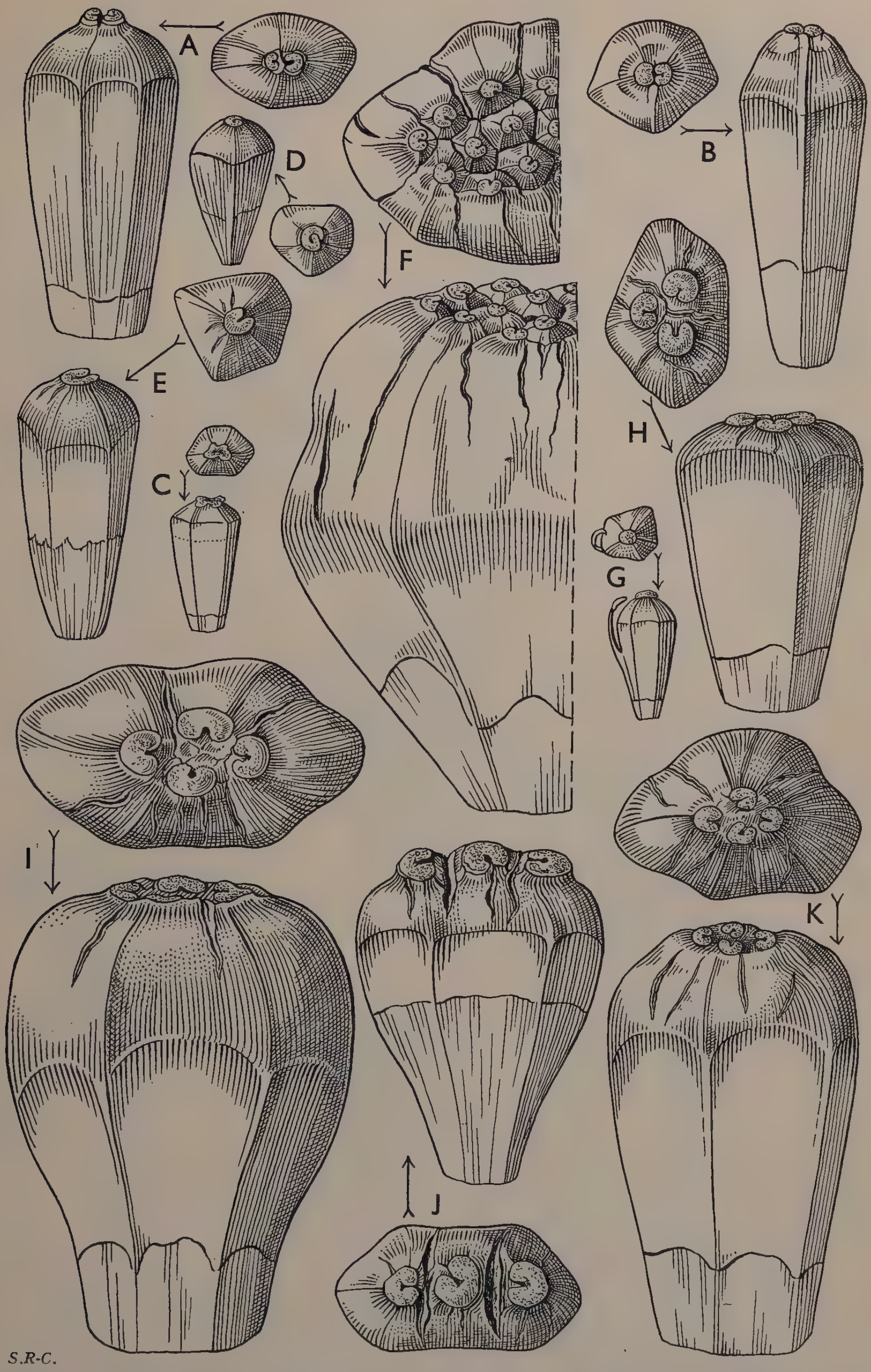
According to observations made on three or four species the syncarp increases very rapidly in size and reaches its maximum development by April or May; the ripe drupes usually fall to the ground towards the end of the year. Germinating drupes have been seen in the following July or August, that is from eighteen to twenty months after fertilization, though the period of dormancy may be considerably extended and the germination of drupes from an individual syncarp or from the same generation may be very irregular. In multilocular drupes such as those of *P. eydouxia*, where the number of potential embryos may be as many as 40–50, it is rare to find more than four or five seedlings produced; an example of multiple germination in a plurilocular drupe is shown in Text-fig. 1C, where four seedlings are seen to be germinating from a single drupe of *P. palustris*. Staminodes have been observed in the syncarp of *P. microcarpus* (Text-fig. 2G) in which a single staminode is fused to the wall of the ovary.

Though no figures are yet available, the germinating capacity of the Mauritius species is extremely low. Young plants or germinating seeds have not been found in the majority of species, even those where both male and female flowers occur in proximity. On reaching maturity the syncarp breaks up into its constituent drupes revealing the fused portion of the drupe, which is usually brightly coloured red, lemon-yellow, or orange, with the odour of rotting pine-apple. No doubt these fruits proved attractive to extinct birds like the dodo or large parrots, and possibly fruit-bats, which assisted in their local distribution. The mesocarp is traversed by a dense mesh of fibres, while the seeds are enclosed by the extremely hard endocarp which is penetrated by the mesocarp fibres and extends across the centre of the drupe in the form of an irregular woody plate perforated on both surfaces by the seed loculi and occupying usually about one-third or a quarter of the drupe. The drupes of most of the Mauritius species sink in water, and during periods of exceptionally heavy rainfall are rolled over the forest floor or down stream-banks, thus obtaining in this way a restricted distribution.

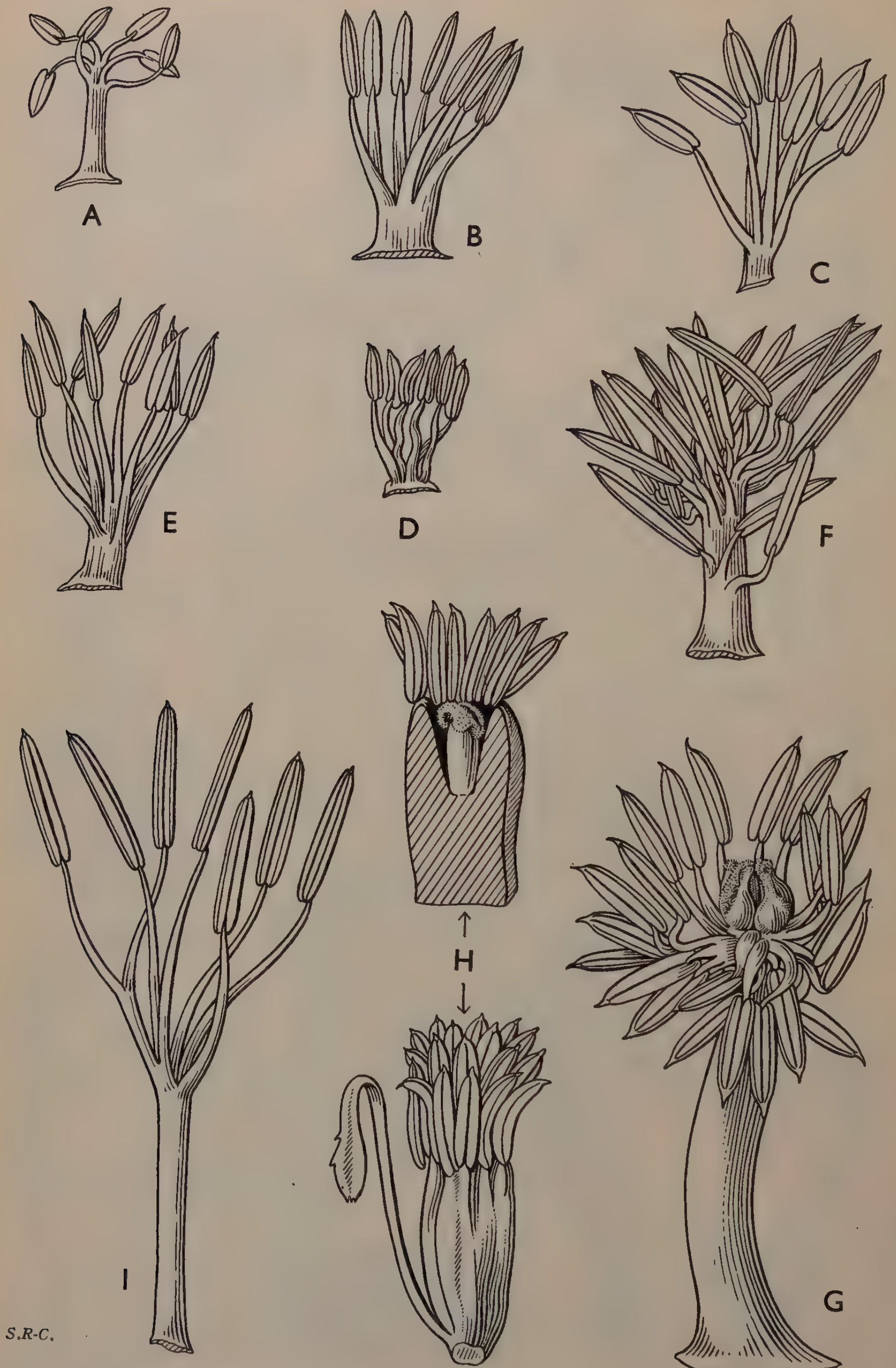
All students of screw-pines have commented on the sporadic flowering of the male plants and the rarity of male flowers; only about one-fifth of the species recorded in Warburg's Monograph include descriptions of the male flowers. Some scraps of a few males of the Mascarene species may be found in herbaria, but no description of the male flowers was given in Balfour's account of the genus in Baker's *Flora of Mauritius and the Seychelles*. In the present paper the males of eight species are figured and described, including those of two new species, and it is possible that the males of several others may be discovered in the near future. It is observed that the male bud expands very quickly, the main axis of the spadix growing with great rapidity, parting the bracts to display the fleshy branching spadix with its numerous yellow sweet-smelling stamens. The pollen is



Text-fig. 1. Drupes of Mascarene *Pandanus*, natural size. A–B, *P. heterocarpus*; C, *P. palustris*, germinating; D, *P. vandermeerschii*; E, *P. barklyi*, form with small fissured drupes; F, *P. barklyi* var. *macrocarpa*; G, *P. barklyi*, typical dome-shaped drupe from large female head; H, *P. sylvestris*; I, *P. purpurascens*.



Text-fig. 2. Drupes of Mascarene *Pandanus*, natural size. A, *P. obsoletus*; B, *P. prostratus*; C, *P. rigidifolius*; D, *P. montanus*; E, *P. sphaeroideus*; F, *P. glaucocephalus*; G, *P. microcarpus*, with staminode; H, *P. carmichaelii*; I, *P. spathulatus*; J, *P. incertus*; K, *P. pyramidalis*.



Text-fig. 3. Stamens of Mascarene *Pandanus*, ×4. A, *P. microcarpus*; B, *P. prostratus*; C, *P. carmichaelii*; D, *P. sphaeroideus*; E, *P. rigidifolius*; F, *P. eydouxia*; G, *P. palustris*, with cluster of abortive ovaries at top of staminal column; H, *P. barklyi*, upper sketch section through staminal column showing abortive ovary, lower sketch group of stamens with bracteole; I, *P. utilis*.

extensively wind-borne, though pollination is probably further assisted by insects, notably earwigs, which are nearly always found crawling about inside the floral bract leaves of both male and female flowers. The whole male inflorescence is very short-lived and in a day or two has blackened and rotted away; this fugacious character may be one reason why the male flowers have so often been overlooked. On the bracteated branches of the spadix the stamens are arranged in clusters or fascicles of varying complexity from the simplest form with few, nearly free, stamens as in *P. sphaeroideus* (Text-fig. 3D) to a complex, more or less umbellate, aggregate of many stamens, well seen in *P. eydouxia* (Text-fig. 3F) and *P. palustris* (Text-fig. 3G) in which filaments of adjacent stamens have become fused to form a staminal column. In some instances the staminal column is elliptical in cross-section, and the vascular strands of the individual filaments composing the column can be clearly seen. Interesting are the male flowers of *P. barklyi* where abortive ovaries sometimes occur in a groove at the top of the staminal column (Pl. **3**, fig. E); here the whole staminal complex with the abortive ovaries is often subtended by a bracteole resembling a minute pandan leaf (Text-fig. 3H). The presence of abortive ovaries has also been observed in *P. palustris* (Text-fig. 3G). Though a statistical analysis would be necessary to confirm the point, the number of stamens in each staminal group in *P. barklyi* appears to run in multiples of three, usually fifteen, eighteen, or twenty-one, indicating the union of adjacent trimerous flowers.

It will be seen that the build-up of both the male and female inflorescences is due to a process of fasciation. In the latter, the solitary carpels of individual female flowers have become united to form syncarps with unilocular drupes characteristic of the section *Sussea*; the adjacent carpels then become fused together to form syncarps with pauci- or multilocular drupes typical of the section *Vinsonia*.

In the same way, in the male inflorescences, fasciation has taken place to produce a staminal cluster, though the number of flowers contributing to the cluster and the degree of fasciation vary considerably from species to species. Although an exact parallel must not be expected, it is noticed that those species with unilocular syncarps have male flowers with few stamens and slight (Text-fig. 3D) or moderate fasciation (Text-fig. 3A), while the species with pauci- or multilocular syncarps have male flowers with a more complex staminal arrangement (Text-fig. 3F, G). Further, the dwarf or slender-growing species usually have a unilocular syncarp, while the stout tree-like forms, for example *P. eydouxia*, have a multilocular syncarp and a complex staminal cluster. These relationships are further discussed in the following section on phylogeny.

Phylogeny and origins

Reference has already been made to the sections into which the genus has been divided by Warburg, Martelli and others. Following this classification, which is based largely on the structure of the stigma and the arrangement and number of carpels, the Mascarene species may be placed in the following sections: *Keura*, represented by the solitary species *P. palustris*; *Sussea*, comprising *P. montanus*, *P. microcarpus*, *P. sphaeroideus*, *P. rigidifolius* and *P. vandermeerschii*, these species all having unilocular drupes with flat, more or less sessile stigmas; and finally *Vinsonia*, with pauci- or multilocular drupes with the carpels either uniseriate or irregularly arranged, with cordate or uniform sessile stigmas; this section includes the remainder and the bulk of the Mascarene species. Warburg founded the section *Barklya* on two Mauritius species, *P. barklyi* and *P. prostratus*, which, according to the material then available, he considered had uniseriate carpels; this is a very variable and artificial character, and in some forms of *P. barklyi* drupes with both uniseriate and irregular carpels may be found in the same syncarp. It is not therefore possible to maintain this section, and these two species may be referred to the section *Vinsonia*.

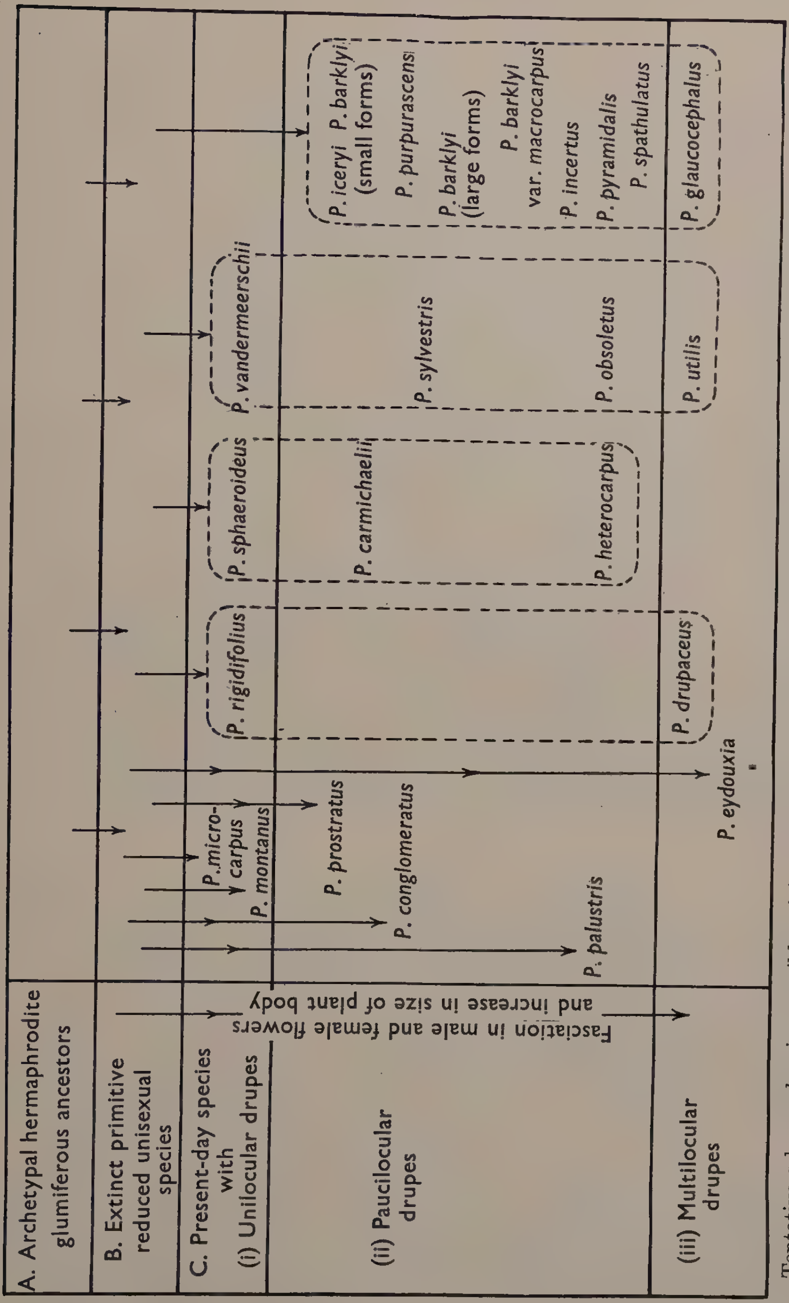
The arrangement of the Mascarene species into these sections is a convenient but artificial arbitrary classification, based largely on the study of herbarium specimens of drupes. With our wider knowledge of the male flowers, vegetative characters, and the habit of the plants in the field it is possible to sort out to some extent the heterogeneous species which have been lumped together in these sections. Further, in attempting an appraisal of the natural relations between the species consideration must be given to the views advanced in the section on life history that the pauci- and multilocular drupes have been derived by fasciation from unilocular types and that a parallel line of development has taken place in the male flower, this increasing complexity in the floral apparatus being accompanied by an increase in the size of the plant body as a whole.

The members of the section *Sussea* show great variation in their habit, male flowers, and the structure of the drupe; they clearly have a polyphyletic origin and are derived from widely differing primitive and now extinct unisexual and unilocular forbears.

In the section *Vinsonia* some of the species are isolated populations which have been evolved from unilocular forms long extinct; other groups of species in this section may show close affinities with each other and with unilocular species of the section *Sussea*. For example, a well-defined aggregate of closely related species is the group including *P. vandermeerschii* (*Sussea*), *P. sylvestris*, *P. obsoletus*, and *P. utilis* (*Vinsonia*). All these have red-spined leaves with drupes truncate at the base and rapidly tapering to the apex which is crowned by the very small stigmas; the habit of young specimens of *P. utilis* and *P. vandermeerschii* is very similar. Then there is the *P. barklyi* complex which is evidently a very labile group, some members having appeared in comparatively recent times; included here are *P. barklyi* and its several forms and varieties, *P. iceryi*, *P. glaucocephalus*, and the more distantly related *P. pyramidalis* and *P. purpurascens*. Curious, too, is the resemblance in general habit and in the red-spined rigid ascending leaves between the elegant little dwarf unilocular species *P. rigidifolius* and its giant counterpart *P. drupaceus*. Another natural group probably includes those species with flat-topped or slightly exerted drupes and often rather large stigmas like *P. carmichaelii*, and the Rodriguez species *P. heterocarpus* which seem to have affinities with the unilocular species *P. sphaeroideus*. Mention must be made here of species with compound female syncarps; these are found in several widely separated sections and not confined to any particular region but scattered through the islands of the western Indian Ocean, examples occurring in Mauritius, the Seychelles, Madagascar and East Africa. Assuming that the prototype pandan flower was a bracteated paniculate hermaphrodite spadix, subsequent segregation of the sexes would produce the branching male spadix which is maintained in all the male inflorescences so far discovered. In the female, contraction of the branches with fusion and fasciation of adjacent flowers would give rise to a compound inflorescence and, at a later stage, suppression and reduction would produce the common form of solitary female syncarp. It is interesting to note that in one Mascarene species, *P. prostratus*, a secondary smaller head is sometimes found on the same peduncle as the main terminal syncarp.

The scheme facing this page summarizes the views expressed above, though it must be regarded purely as a preliminary essay unsupported by any knowledge of the cytogenetics or anatomy of the species; groups of related species are arranged to the right of the scheme and enclosed by dotted lines, the remainder are placed in an arbitrary manner to the left, the order of arrangement not necessarily implying any definite relationship.

The geographical distribution of the sections and subsections described above has some significant features. Thus the *P. vandermeerschii*-*P. utilis* subsection is scattered through the Mascarenes and Madagascar and not confined to any particular island; the *P. barklyi* subsection however is much more localized, being of more recent origin. In the Warburgian section *Sussea* the Mauritius species *P. rigidifolius* and *P. microcarpus* are more closely related to the Réunion *P. montanus* and associated Madagascar species than to the other Mauritius species of this section; this suggests that these related species are the descendants of more primitive types with a former wide distribution which have persisted to the present day, whereas the more advanced pauci- and multilocular types became differentiated and evolved within the present restricted geographical area in which they are now found.



Tentative scheme showing possible origin and relationships of Mascarene pandans (for further explanation see text, page 12)

The views advanced above concerning the phylogeny of the Mascarene pandans, taken in conjunction with their geographical distribution, permit us to present a brief review of their past history and origins which, though partly conjectural, may be considered to have a basis of reality in its broad outlines. We may suppose that the archetypal forms from which the present-day species have been derived were small creeping or erect and, in some cases, epiphytic aloe-like plants with paniculate inflorescences producing succulent drupaceous or baccate fruits similar to those of existing primitive Liliaceae, like *Cohnia* and *Astelia*, genera with remarkable oceanic distribution. These paleo-pandans, as we may call them, constituted a complex assemblage of species which were able to adapt themselves to a wide range of climatic and edaphic conditions and formed extensive consocies in different plant communities extending from littoral to montane regions.

Since the publication of Wegener's Drift Theory in 1912 a large and impressive body of evidence has accumulated to indicate that extensive modifications and changes have taken place in the relative positions of the great land masses of the Earth, and it is not too premature to postulate the former existence of Gondwana, the great southern continent of Suess, over the eastern regions and neighbouring islands of which the succulent drupes of our paleo-pandans were distributed far and wide by birds. Subsequent fragmentation, separation, and drift of the islands then took place, dissemination of the fruits became restricted and localized, and differentiation into the ancestors of the endemic forms we know to-day took place.

Guppy (1906) suggested that the distribution of pandans was significantly assisted by the extinct Columbae (dodo and solitaire) in the Mascarene region and the Megapodes or fruit pigeons in the Pacific; though this distribution was probably local rather than regional in character as the same factors, namely isolation and insularity, which were operating to produce the endemic pandans were also responsible, at a later period, for the evolution and survival of the peculiar flightless birds. However, we may certainly agree with Guppy when he says that 'it is evident from the endemic character of most of the species of *Pandanus* in oceanic islands that, except with a few widely spread littoral species, the dispersal of the genus has been for ages suspended'; and it may be added that no existing means of dispersal can account for the present distribution of the genus in the Mascarene region.

ANNOTATED DESCRIPTION OF THE SPECIES

In the citation of material examined in different herbaria the following abbreviations are used: Hb. Kew: Herbarium, Royal Botanic Gardens, Kew; Hb. Mus. Brit.: British Museum (Natural History), London; Hb. Mus. Par.: Muséum National d'Histoire Naturelle, Paris; Hb. Maur. Inst.: Mauritius Institute, Port Louis, Mauritius; Bot. Mus. Fl.: Istituto Botanico, University of Florence.

The collections we have made in the field, including the type material of the new species, have been deposited in the herbarium of the Mauritius Institute. It has not been possible to identify the type specimens of most of the earlier described species.

PANDANUS L. (Mascarene species)

Unisexual shrubs or low trees with creeping, ascending, or upright stems ringed with annulate leaf-scars and often producing aerial or stilt-roots; pneumatophores sometimes present. Leaves long, narrow, acute, with spinous keel and margins, three-ranked and spirally arranged in dense tufts at the ends of the solitary or whorled branches. Flowers without a perianth; the male inflorescence a large paniculate bracteated spadix with numerous stamens usually in fasciculate groups or bundles spirally or otherwise disposed on the rachis. Anthers basifixed, oblong, and often apiculate. Female flowers with many connate one-celled ovaries often confluent into clusters and forming a subsessile or pedunculate, simple (or, in one species, compound) head enclosed by fleshy or leaf-like bracts. Ovules solitary, anatropous, parietal, giving rise to a minute embryo immersed in the oily endosperm. Fruit a large, globose, ovoid, or cylindrical syncarp breaking up on maturity into numerous one- or many-celled pulpy or fibrous drupes with woody endocarp.

Artificial key to the species

1′. Female heads compound. 7. *conglomeratus.*
1″. Female heads solitary.
2′. Heads large, up to 20–30 cm. diam., comprising 20–60 drupes exceeding 7–8 cm. in length.
3′. Drupes 3–6-locular, with large fleshy oblique stigmas 6–10 mm. broad. 1. *palustris.*
3″. Drupes 10–50-locular, with flat reniform or cordate stigmas 3–4 mm. broad.
4′. Leaves 12 cm. broad, rigid, with red marginal spines and stigmas placed in apical depression of drupes. 8. *drupaceus.*
4″. Leaves 6–8 cm. broad, drooping, with white or brown marginal spines and stigmas scattered over surface of flat-topped drupes.
5′. Drupes free in the upper half or two-thirds, 20–50-locular, up to 12–14 cm. broad. 9. *eydouxia.*
5″. Drupes free in the upper third or quarter, 12–20-locular, up to 7–8 cm. broad. 10. *glaucocephalus.*
2″. Heads rarely exceeding 20 cm. diam. with 50–500 drupes up to 6–7 cm. long.
3′. Drupes unilocular, more rarely 2–3-locular, seldom exceeding 3–4 cm. long by 1·5 cm. broad, stigmas variously shaped and rarely exceeding 3 mm. broad.
4′. Stigmas oblique, stipitate, drupes free in the upper half, the apex deeply cleft between the stigmas. 6. *vandermeerschii.*
4″. Stigmas flat, reniform or annulate, subsessile.
5′. Leaf spines white or brown, drupe up to 3·5–4 cm. long. 4. *sphaeroideus.*
5″. Leaf spines red or orange, drupes seldom exceeding 2 cm. long.
6′. Stigmas annulate, exposed portion of drupe dome-shaped or pyramidal. 2. *montanus.*
6″. Stigmas reniform or cordate, exposed portion of drupe flat or convex.
7′. Peduncle twisted and recurved, leaves drooping, drupes up to 2·5 cm. long. 3. *microcarpus.*
7″. Peduncle short and erect, leaves stiff and rigid, drupes up to 1·5 cm. long. 5. *rigidifolius.*
3″. Drupes 2–10-locular, rarely unilocular, usually exceeding 3–4 cm. long by 1·5 cm. broad, stigmas not stipitate.
4′. Stigmas 5–8 mm. broad, rarely 3–4 mm., carpels uniseriate or irregular.
5′. Exposed portion of drupes flat and angular. Drupes slightly compressed. 11. *carmichaelii.*
5″. Exposed portion of drupes dome-shaped or pyramidal.
6′. Drupes 4–8-locular, stigmas fleshy, somewhat oblique. 12. *macrostigma.*
6″. Drupes 2–3-locular (rarely up to 10-locular), stigmas flat.
7′. Drupes 6–7 cm. long by 4–5 cm. broad. 13. *spathulatus.*
7″. Drupes 4–5 cm. long by 3–4 cm. broad. 14. *incertus.*
4″. Stigmas 1–4 mm. broad.
5′. Carpels usually irregular, rarely uniseriate.
6′. Apex of free portion of drupe with a flat or depressed space (areole) on which the stigmas are placed.
7′. Leaf spines red, areole bordered with a distinct corky margin. 15. *heterocarpus.*
7″. Leaf spines white or brown, areole without a distinct corky margin.
8′. Peduncle strongly recurved, drupes usually 5·6 cm. long, exposed portion of drupe deep shining green, joined portion lemon-yellow when ripe. 16. *pyramidalis.*
8″. Peduncle suberect, drupes very variable in size and shape, 3–6 cm. long, exposed portion of drupe brown, purple or glaucous-grey, joined portion red or greenish purple when ripe. 17. *barklyi.*
8‴. Female head pendulous with peduncle arising from main trunk, drupes 3·0–3·5 cm. long. 18. *iceryi.*

6″. Apex of free portion of drupe usually without an areole.
  7′. Heads very variable in shape and size up to 20 cm. diam. with 100–200 drupes. . **19.** *utilis.*
  7″. Heads small, rarely exceeding 10 cm. diam., with 20–50 drupes.
    8′. Heads 7–10 cm. diam., drupes 3–4 cm. long by 2·0–2·5 cm. broad. **20.** *purpurascens.*
    8″. Heads 6–7 cm. diam., drupes 2 cm. long by 1·5–2 cm. broad. **21.** *sylvestris.*
5″. Carpels usually uniseriate, rarely irregular.
6′. Drupes narrow, usually twice as long as broad, rarely more than 3-locular, up to 350 in a single head, apex of drupe without an areole.
  7′. Leaf spines red, heads drooping, globose, depressed at apex; exposed portion of drupe dark green with a red or purple ring at base, joined portion of drupe red when ripe. **22.** *obsoletus.*
  7″. Leaf spines white or brown, heads suberect, oblong-cylindrical exposed portion of drupe glaucous grey or green, joined portion of drupe lemon-yellow when ripe. **23.** *prostratus.*
6″. Drupes usually less than twice as long as broad, 3–8-locular, up to 150 in a single head, apex of drupe sometimes areolate.
  7′. Drupes very variable in number, shape, size and colour, 50–150 in a head, 3·5–6 cm. long by 2·5–3·5 cm. broad, the larger drupes free in the upper fourth or fifth, the smaller free in the upper third, sometimes deeply fissured between the stigmas. **17.** *barklyi.*
  7″. Drupes less than 50 in a head, 5 cm. broad, free in the upper half. **17***a.* *barklyi* var. *macrocarpus.*

1. **P. palustris** Thouars in *Bull. Sci. Soc. Phil., Paris,* **186** (1808) et in Desv. *J. Bot., Paris,* **1**, 48 (1808); Lam. *Encycl. Bot.,* Suppl., **1**, 577 (1810); Spreng. *Syst. Veg.* **3**, 898 (1826); Bojer, *H.M.* 301 (1837); Kunth, *Enum. Pl.* **3**, 96 (1841); Steud. *Nom. Bot.* **2**, 251 (1841); Voigt, *Cat. Hort. Calc.*, 683 (1845); Kurz in Seem. *J. Bot., Lond.*, **5**, 133 (1867); Balf. f. in Baker, *F.M.S.* 402 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 57 (1878); Warburg in *Pflanzenr.* Pand. 45 (1900); Martelli in *Webbia*, **4**, 26, t. 35 f. 1–2 et t. 36 f. 1–3 (1913).
'Baquois des marais' (Lamarck), 'Vacoas de Chine.'

Erect tree, 8–10 m. high, usually solitary, the main stem terminating in a dense crown of drooping leaves, the youngest leaves only erect, with a thick shag of old leaves and leaf-bases below the crown. Stem 20–25 cm. diam., brownish grey with short spiny warts and close-set inconspicuous leaf scars. Leaves 1·75–2 m. long by 10–12 cm. broad, pale green, smooth, waxy beneath, narrowing gradually to an acuminate apex, margins armed throughout with minute white or pale yellow, often brown-tipped, spines. Pneumatophores abundant, stilt roots numerous, arising from all parts of the stem, particularly near the base. Mature female head globose with 40–60 drupes, dull greenish brown, up to 30 cm. diam., clasped by large persistent bract leaves which are boat-shaped in the lower third and narrow abruptly upwards into a long linear apex. Drupes 4–6-locular, 12–16 cm. long by 6–7 cm. broad, free in the upper quarter or fifth; the free portion deeply grooved between the pyramidal apices of the carpels, the joined portion lemon-yellow when ripe. Stigmas irregular, fleshy, oblique, 6–10 mm. broad. Mesocarp with dense black fibres penetrating the woody endocarp. Male spadix often exceeding 1 m. in length, with a stout white fleshy rachis bearing up to 15–25 bracteated branches and three or more empty bract leaves 100–120 cm. long at base of spadix. Bract leaves white, boat-shaped in the lower third, the upper portion linear-acuminate, becoming progressively smaller towards apex of rachis. Lateral branches of spadix flat or trigono-elliptical in section, 10–40 cm. long by 1·5–4·0 cm. broad. Staminal columns loosely scattered on the surface of the rachis but more frequent on the abaxial surface. Stamens 20–50, crowded at the top of an elliptical or circular column 18–20 mm. long by 4–6 mm. broad, the free portion of the filaments 1–3 mm. long; anthers 4–5 mm. long by 1–1·5 mm.

broad with an acuminate apex; top of staminal column sometimes crowned with abortive ovaries.

Text-fig. 1C; Text-fig. 3G; Pl. **1**, fig. D; Pl. **2**, fig. D; Pl. **3**, figs. A, F.

Exsiccata. *Horne* 1875 *Barkly*, Curepipe (Hb. Kew); *V/3059*, *V/3186*, Curepipe ♂ flower, 16 January 1947; *V/3185*, Perrier 9 January 1947; *V/1461*, Mare-aux-Vacoas (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. This species is usually restricted to streams and permanently water-logged marshes in the uplands, and is said to have occurred in dense stands in the marshy area since converted into the Mare-aux-Vacoas reservoir.

It is curious that the remarkable male inflorescence of this species (Pl. **3**, fig. A) should have received so little comment from earlier botanists and collectors. The flower first makes its appearance as a large erect terminal bud, the staminal branches hidden by closely imbricated boat-shaped bract leaves. The axis of the spadix or rachis then elongates very rapidly, separating the bracts and exposing the flat creamy-white branches of the drooping spadix with their scented stamens. The flower is very short-lived, and within a few days the huge black foetid-smelling spadix collapses and falls to the ground. In its prodigal formation of pollen *P. palustris* equals or exceeds that of the larger male flowers of many palms. Another peculiar feature of this species is the short ascending pneumatophore-like processes which often beset the lower part of the main stem.

Germinating drupes are occasionally found but are not common; an unusual case is illustrated in Text-fig. 1C which shows four germinating embryos derived from a five-locular drupe, the young leaves of which are emerging from the base of the drupe; the epidermal tissues have rotted away exposing the coarse black fibres of the mesocarp.

P. palustris belongs to the section *Keura* characterized by the large fleshy stigmas crowning the summits of the carpels.

2. **P. montanus** Bory, *Voy.* **1**, 313 (1804); Balf. f. in *J. Linn. Soc.* (*Bot.*), **17**, 53 (1878); Cordem. *Fl. Réunion*, 138 (1895); Warburg in *Pflanzenr.* Pand. 65, figs. 8H, 17F–H (1900); Martelli in *Webbia*, **4**, 25 (1913). *P. erigens* Thouars in *Bull. Sci. Soc. Phil.*, *Paris*, 185 (1808) et in Desv. *J. Bot.*, *Paris*, **1**, 46 (1808); Lam. *Encycl. Bot.*, Suppl., **1**, 577 (1810); Kunth, *Enum. Pl.* **3**, 97 (1841); Kurz in Seem. *J. Bot.*, *Lond.*, **5**, 130 (1867).

'Vacoas marron', 'Baquois redressé' (Lamarck).

Low, much branched, slender tree reaching 6–8 m. Leaves 25–50 cm. long by 2 cm. broad. Female head oblong, erect at first then drooping; peduncle 8–10 cm. long. Drupes 2–2·5 cm. long by 0·7–1·0 cm. broad, 1–2-locular, free in the upper quarter, the free portion dome-shaped and red or dark brown when ripe. Stigmas annulate 2–3 mm. broad. Male flower unknown.

Text-fig. 2D.

Exsiccata. d'Emmerez de Charmoy (Hb. Maur. Inst.). The specimen in the Paris Museum labelled *Sussea conoidea* and supposed to have been collected by Pervillé in Madagascar probably comes from Réunion, and Martelli refers it to *P. montanus*.

Distribution. Réunion, endemic. On the high plateau of the interior, particularly in thickets and native scrub-lands of the Plaine des Palmistes where it is often a dominant species.

According to Balfour (1878) this species occurs also in Madagascar, but Warburg considers the Madagascar plant, which is much more robust with larger leaves and female heads, sufficiently distinct to warrant specific rank and has assigned to it the name *P. bakeri* (Warburg, loc. cit. p. 65). *Sussea conoidea* Gaudich. (loc. cit. t. 24) probably represents *P. bakeri* and not the Réunion species. Warburg refers *Sussea microcarpa* Gaudich. (loc. cit. t. 25) to *P. microcarpus* Balf. f., but the characteristic annulate stigmas so clearly depicted in Gaudichaud's figure leave little doubt that this is really *P. montanus* or a closely allied Madagascar species. Warburg's figure also indicates the annulate or horse-shoe-shaped stigma which is not found in any other Mascarene species. The four species, *P. montanus* Bory (Réunion), *P. bakeri* Warb. (Madagascar), *P. myriocarpus* Baker (Madagascar), and *P. microcephalus* Baker (Madagascar), form a very closely related group from which *P. rigidifolius* Vaughan & Wiehe (Mauritius) and *P. microcarpus* Balf. f. (Mauritius) are not far removed, and it is interesting to note that all these widely scattered species belong to a group or section (*Sussea*) with small unilocular drupes in which fasciation has not taken place to produce the multilocular drupes of the higher types.

3. **P. microcarpus** Balf. f. in Baker, *F.M.S.* 396 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 52 (1878) excl. syn.; Warburg in *Pflanzenr.* Pand. 65 (1900); Martelli in *Webbia*, **4**, 23 (1913).

A slender freely branching shrub or low tree reaching 5–6 m. high, ultimate branches often less than 3 cm. diam. Main trunk 8–10 cm. diam. with smooth brownish grey bark sparsely clothed with blunt spines; stilt roots 3 cm. diam. confined to base of stem. Leaves 30–50 cm. long by 1–3 cm. broad, dark yellow-green, waxy on both surfaces, narrowing gradually to an acuminate apex. Margins and midrib of leaf closely beset throughout with conspicuous red spines. Female head red or purple, egg-shaped or cylindrical, up to 9 cm. long by 7 cm. broad with 75–200 drupes; peduncle twisted and recurved, 20 cm. long, clothed with persistent leaf-like bracts. Drupes unilocular, rarely 2–3-locular, 2–3 cm. long by 1–1·5 cm. broad, slightly compressed or irregularly 5–6-angled. Apex flat, convex or more rarely pyramidal, stigmas flat, reniform, 2–2·5 mm. broad. Male spadix up to 50 cm. long, very slender and drooping, the main rachis flattened, 0·5 cm. broad, bearing 8–12 lateral branches. Bract leaves boat-shaped, white, or pink-tinged, and bearing minute red spines on margins and under surface of midrib. Lateral branches of rachis 5–8 cm. long, densely beset with the brownish staminal columns. Stamens in bundles of 4–10, the filaments joined in the lower half or third to form a short staminal column 1–2 mm. long. Free portion of filament up to 5 mm. long.

Text-fig. 2G; Text-fig. 3A; Pl. **2**, fig. G.

Exsiccata. *Horne*, 1875 (Hb. Kew); *V/3111* Curepipe Botanic Gardens 24 June 1946; *V/3015* Rivière Sèche (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Probably at one time confined to river banks in regions of medium rainfall. It is not possible to define its original distribution with any accuracy because the native vegetation of the river reserves has been largely destroyed and replaced by exotic species.

P. microcarpus is readily distinguished from other species with unilocular drupes by the small purple syncarp borne on a twisted peduncle. A very interesting feature of this species is the occasional occurrence of staminodes. These have not been found in any other Mascarene species and, indeed, are very rare in the genus as a whole. In Gaudichaud's Atlas a species is figured (*Sussea microstigma* Gaudich. loc. cit. t. 38) showing a unilocular ovary or young drupe with six or more staminodes arising from its base, but no reference to, or description of, these structures can be traced in the literature apart from the description by Warburg of Gaudichaud's drawing. In *P. microcarpus* the female flower bears a solitary staminode which does not arise from the receptacle or from the base of the hexagonal ovary, but is fused about halfway down to one of the angles of the latter and bears a basifixed anther projecting 2–3 mm. above the surface of the syncarp (Text-fig. 2G).

4. **P. sphaeroideus** Thouars in *Bull. Sci. Soc. Phil., Paris*, **185**, 40 (1808) et in Desv. *J. Bot., Paris*, **1**, 46 (1808); Lam. *Encycl. Bot.*, Suppl., **1**, 517 (1810); Kunth, *Enum. Pl.* **3**, 97 (1841); Kurz in Seem. *J. Bot., Lond.*, **5**, 130 (1867); Balf. f. in Baker, *F.M.S.* 386 et in *J. Linn. Soc.* (*Bot.*), **17**, 61 (1878); Warburg in *Pflanzenr.* Pand. 66, fig. 16, N–P (1900); Martelli in *Webbia*, **4**, 31 (1913). *P. globuliferus* Thouars loc. cit. 185, et loc. cit. 47, Lam. loc. cit. 577; Spreng. *Syst. Veg.* **3**, 898 (1826); Bojer, H.M. 301 (1837); Kunth, loc. cit. 97; Kurz, loc. cit. 131.

A low tree 5–7 m. high with slender branches. Stem 10–12 cm. diam. with smooth pinkish grey bark and leaf-scars visible only on the younger parts of the ultimate branches which are 4–5 cm. diam. Stilt roots often numerous and sometimes reaching apex of stem. Leaves 75–115 m. long by 5–6 cm. broad, yellow-green, reduplicate, mostly stiff and ascending, tapering suddenly to a blunt apex. Marginal spines pale yellow or white becoming brown-tipped, close set; lower surface of midrib with spines in the upper third. Female head variable in size, globose, up to 12 cm. diam., clasped by the tristichous bract leaves. Drupes 125–250, unilocular, not compressed, sharply 4–6-angled, 3·5–4 cm. long by 1·5 cm. broad, the free portion flat or convex, pale glaucous-green, with a brown corky apex, stigmas flat, sessile, reniform, up to 4 mm. broad. Male spadix white, fleshy, 30–40 cm. long, rachis triangular in section, 0·5 cm. diam., bearing 8–10 lateral branches. Basal bract leaves 35–50 cm. long by 3–4 cm. broad, greenish white, with spinous margins, terminal bract leaves 3 cm. long by 1 cm. broad, white, smooth, deciduous. Stamens in bundles of 4–10, filaments twisted and contorted, 3–5 mm. long, free or united near the base to form a short staminal column; anthers 3·0 mm. long by 0·75 mm. broad.

Text-fig. 2E; Text-fig. 3D; Pl. **1**, fig. C; Pl. **2**, fig. C; Pl. **3**, fig. G.

Exsiccata. *Horne*, *Bouton*, 14 November 1864 (Hb. Kew); *Cuming*, 1864; *Cutler* (Hb. Mus. Brit.). *V/3014*, *V/3151*, *V/3121* A, *V/3135*, *V/3123* Rivière Bémanique 2 January 1947; *V/3133*, stream near La Marie water-works 19 October 1946 (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Common in the uplands on river banks in marshes and exposed indigenous thickets.

A very variable species according to habitat. When growing on the exposed plateau of Les Mares and Le Pétrin it forms a low dense thicket or scrub 1–2 m. high with leaves little more than a foot long, and it is frequently one of the dominant constituents of the indigenous scrub associes of this area. A form with stout, smooth, fawn-coloured stems, large leaves and female heads up to 15 cm. diam. is sometimes found on stream banks at Midlands and Cluny.

5. **Pandanus rigidifolius** Vaughan & Wiehe sp. nov.

Frutex 2–3 m. altus, saepe caespitosus, trunco tenui 6–8 cm. diam. Folia rigida, crassa, 75 cm. longa, 6 cm. lata, induplicata et profonde canaliculata, rubro-marginata dense et spinis crassis brevibus rubris in margine armata. Syncarpium solitarium, oblongum, 7–8 cm. diam., pedunculo brevi erecto; drupae 200–220 in syncarpio, vulgo uniloculares, 1·6–2·0 cm. longae, 0·8 cm. latae, apice libero plano vel sub-convexo vertice stigmate reniformi 2–2·5 mm. lato coronato. Spadices masculae 35–40 cm. longae; spathae naviculares, dorso-carinatae. Stamina ad 6–9 in fascicula, tertia inferiori parte in columnam adnata; antherae 3 mm. longae apice acuminatae.

Low-spreading or straggling shrub, rarely exceeding 2–3 m. high, forming large dense clumps; main stem up to 8 cm. diam., much branched, marked with irregular fissures. Stilt roots, 2 cm. diam., slender, scattered, and extending to the ultimate branches. Leaves up to 75 cm. long by 6 cm. broad, deep glaucous green, waxy on both surfaces, strongly reduplicate, very stiff and rigid, narrowing abruptly to an obtuse apex, marginal spines closely set, red or orange. Female head oblong or obconical 7–8 cm. diam. with 200–220 drupes, peduncle short and erect, the head clasped by the tristichous bracts. Drupes unilocular, more rarely 2-locular, 4–5-angled, 1·6–2·0 cm. long by 0·8 cm. broad, united nearly to the top, apex flat or somewhat convex, joined portion red when ripe. Stigmas 2–2·5 cm. broad, sub-sessile with free crenulate margins. Male spadix 40–55 cm. long, main rachis cylindrical 0·5 cm. diam., bearing up to twelve triangular lateral branches which are 9–12 cm. long. Basal bract leaves boat-shaped, reduplicate, armed with yellow or red spines, up to 30 cm. long; apical bracts 6 cm. long by 0·75 cm. broad, white, plicate. Filaments of stamens fused in the lower third forming a short fasciated column 1·5–2·5 mm. long, bearing 6–9 stamens; free portion of filaments 4–5·5 mm. Anthers 3 mm. long with an acuminate apex.

Text-fig. 2C; Text-fig. 3E; Pl. **3**, fig. J; Pl. **4**, fig. D.

Exsiccata. *V/3132* type, *V/3150*, Le Pétrin–Les Mares road (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Forms low dense clumps in marshy ground above 1800 ft. in the neighbourhood of Le Pétrin and Les Mares.

This species, characterized by its dwarf habit, small rigid red-spined leaves and very small unilocular drupes, has some affinities with the Mauritius species *P. microcarpus* Balf. f., but it is probably more closely allied to the Madagascar *P. microcephalus* Baker and associated species.

6. **P. vandermeerschii** Balf. f. in Baker, *F.M.S.* 389 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 65 (1878); Warburg in *Pflanzenr.* Pand. 63, fig. 17, A–E (1900); Martelli in *Webbia*, **4**, 36 (1913).

Low tree, 6–8 m. high, usually growing in clumps and sometimes forming small thickets. Main stem 20–25 cm. diam., freely branched, the ultimate branches often descending and terminated by drooping, fan-shaped tufts of leaves. Bark pinkish grey, sparsely armed with wart-like spines. Stilt roots 6–7 cm. diam., arising from base of trunk. Leaves 50–75 cm. long by 4–5 cm. broad, tapering gradually from the base, marginal spines orange-red. Female head trigono-globose or depressed at the apex 14–16 cm. diam. with 250–450 drupes; peduncle pendulous 30–40 cm. long. Drupes up to 3 cm. long by 1–1·5 cm. broad, 1–4-locular, carpels usually uniseriate, more rarely scattered, free in the upper half, the exposed portion of drupe steeply conical or fusiform, deep green, with a red band at the base, joined portion truncate, pale yellow when ripe. Summit of drupe deeply cleft between the oblique stigmas which are less than 2 mm. broad. Male flower unknown.

Text-fig. 1D; Pl. **1**, fig. E.

Exsiccata. *H. Barkly*, Round Island; *H. H. Johnston*, Ile Vakois and Round Island (Hb. Kew and Hb. Mus. Brit.); coll. Richard (Hb. Mus. Par.); *Viader*, Flat Island; *Wiehe*, Pointe Lascar (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. This species is widely distributed round the coast and on many of the islets bordering the mainland; it is recorded by Horne (1887) from Flat Island, and Johnston (1894, 1895) notes its occurrence on Ile Vakois near Mahebourg and Round Island.

It is evident that Warburg's figure and description in the *Pflanzenreich* have been made from dried material; he refers to the joined portion of the drupes as 'Sensim angustatae saepe fere pedicellatae et haud contiguae'. In living specimens the base of the drupes is contiguous, but considerable shrinkage and distortion take place on drying.

It is unlikely that *Fouilloya maritima* Gaudich. (loc. cit. t. 26, figs. 21–24) is synonymous with *P. vandermeerschii* as Balfour suggested, though it is evidently a closely allied species.

7. **P. conglomeratus** Balf. f. in Baker, *F.M.S.* 403 (1877) et *J. Linn. Soc.* (*Bot.*), **17**, 44 (1878); Warburg in *Pflanzenr.* Pand. 57 (1900); Martelli in *Webbia*, **4**, t. 23, figs. 5–7 (1913).

A small tree, 4–5 cm. high with slender semi-decumbent trunk sparingly branched. Leaves 1–4 m. long by 5–12 cm. broad, narrowing gradually to an acuminate apex, pale green, with midrib and margins armed with long white ascending spines. Female inflorescence pendulous, up to 60 cm. long, heads 8–12, sessile, oblong or cylindrical, 12–20 cm. long by 7–9 cm. broad, containing about 70 drupes. Drupes 3–6-locular, 2–3 cm. long by 1·5–2 cm. broad, slightly compressed, 5–6-angled, free in the upper third or fourth, the free portion dome-shaped or pyramidal, the apex often with a flat or depressed areole ringed by the very small oblique, obscurely mucronate stigmas which are 1·0–1·5 mm. broad. Male flower unknown.

Pl. **2**, fig. B.

Exsiccata. *F. Bijoux*, Fressanges 1909 (Hb. Mus. Par.).

Distribution. Mauritius, endemic, Rivière Eau Bleue near Midlands and Fressanges, and probably restricted to stream banks and marshes in the uplands.

The above description is based on that given by Balfour in Baker (loc. cit.), somewhat modified in accordance with details observed in a small collection of dried drupes and in an old photograph (Pl. **2**, fig. B). We have not seen the material said to have been collected at Midlands and Beau Bassin by Bouton and Horne. *P. conglomeratus* is the only species in the Mascarene Islands possessing a compound female inflorescence, and it is unfortunate that no living plants have been found in recent years; in consequence very little is known about its habit or vegetative characters. Balfour suggested that this species is identical with *P. reflexus* (q.v.); there is indeed a remarkable resemblance between the dried drupes of these two species both in their general sculpturing and the disposition of the stigmas, but a definitive judgement is difficult without examination of the plants in the field. Several near relatives of this species occur in Madagascar and East Africa, and one species with a compound female head, *P. multispicatus*, is endemic in the Seychelles. Some drupes in the Paris Museum, said to have been collected by Gaudichaud in Réunion and referred to *P. purpurascens* by Martelli, closely resemble *P. conglomeratus*.

8. **P. drupaceus** Thouars in *Bull. Sci. Soc. Phil., Paris*, **184** (1808) et in Desv. *J. Bot., Paris*, **1**, 45 (1808); Lam. *Encycl. Bot.*, Suppl., **1**, 576 (1810); Spreng. *Syst. Veg.* **3**, 898 (1826); Bojer, *H.M.* 302 (1837); Kunth, *Enum. Pl.* **3**, 96 (1841); Steud. *Nom. Bot.* **2**, 251 (1841); Voigt, *Cat. Hort. Calc.* 683 (1845); Kurz in Seem. *J. Bot., Lond.*, **5**, 132 (1867); Balf. f. in Baker, *F.M.S.* 400 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 45 (1878); Warburg in *Pflanzenr.* Pand. 56, fig. 15A (1900); Martelli in *Webbia*, **4**, 12 (1913). *P. strigilis* Carm. ex Balf. f. loc. cit.

Shrub or low tree branching freely, the lateral branches often decumbent, trailing, and rooted; stems 12–15 cm. diam. with a scarious pale grey bark marked with longitudinal and transverse fissures. Stilt roots few 1 cm. diam. confined to base of stem. Leaves flat, yellowish green, 100–125 cm. long by 12 cm. broad, very stiff and erect, recurved towards the tip and narrowing rapidly to the acute boat-shaped apex. Marginal leaf spines orange or red, confined to the upper half or quarter of leaf. Female head 20–25 cm. diam. with 20–30 drupes; peduncle very short and erect. Drupes 6–12-locular, 10–12 cm. long by 6–8 cm. broad, 5–6-angled, slightly compressed, waxy purple, free in the upper half or third. Stigmas reniform, flat, 3–4 cm. broad, placed in an apical depression of the drupe. Male flower unknown.

Pl. **1**, fig. A; Pl. **2**, fig. E; Pl. **4**, fig. G.

Exsiccata. *Bouton, Horne* 1875 (Hb. Kew); *Cuming* 1864 (Hb. Mus. Brit.). F. 4417 (Hb. Mus. Par.). *V/3072* Plaine Champagne, 14 June 1947; *V/3072a*, Midlands (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Spread through the uplands in localities with high rainfall, usually on the borders of swamps and marshes, but often colonizing rocky or impoverished ground.

A well-defined species easily recognized by its broad flat erect red-spined leaves and large head. The illustration in Warburg's Monograph is typical. Male plants have been found but with flowers too old for examination. *Vinsonia drupacea* Gaudich. (loc. cit. t. 34, figs. 8–10) is probably the Madagascar species *P. boucheanus* C. Koch.

9. **P. eydouxia** Balf. f. in Baker, *F.M.S.* 401 (1877) et in *J. Linn. Soc.* **17**, 46 (1878); Warburg in *Pflanzenr.* Pand. 55, fig. 15B (1900); Martelli in *Webbia*, **4**, 13 (1913); *Eydouxia macrocarpa* Gaudich. in *Bot. Voy. 'Bonite'*, t. 18, figs. 1–6 (1841); Ad. Br. in *Ann. Sci. Nat.* (6), **1**, 291 (1875).

A tree 10–12 m. high, freely branching to form a wide dome-shaped canopy. Main stem up to 20–25 cm. diam., decumbent or creeping at the base, with slate-grey, rough, fissured bark; leaf scars reddish brown, conspicuous on young branches; stilt roots confined to base of stem. Leaves 115–170 cm. long by 6·5–8 cm. broad, yellowish green with a brown base tapering gradually to an acute apex; marginal spines small, white becoming yellow or brown, lower surface of midrib with minute spines in upper two-thirds. Female head globose 20–25 cm. diam. with 15–25 drupes clasped by large stiff persistent trigonous bracts, boat-shaped in the lower half and produced into a long tapering apex. Peduncle short, erect, clothed with closely set leaf-like bracts. Drupes 20–50-locular, 8–12 cm. long by 6–14 cm. broad by 3–6 cm. deep, very variable in shape, free in the upper half or two-thirds, the joined portion orange-red when ripe. Stigmas flat, reniform, 3–4 mm. broad, scattered over the flat top of the drupe and separated by shallow corky fissures. Male spadix up to 80 cm. long, the main rachis white, fleshy, 2·5–3 cm. diam., bearing 10–15 lateral bracteated branches becoming progressively shorter towards the apex. Lower bract leaves 50–70 cm. long, keeled and boat-shaped towards the base, becoming linear and spinous in the upper half or two-thirds; upper or terminal bract leaves white, linear or oblong, often less than 5 cm. long. Lateral branches flattened or elliptical in section 6–18 cm. long by 3–5 cm. broad, densely clothed with stamens. Staminal column 6 mm. long by 2 mm. broad, bearing 8–12 stamens, the free portion of the filaments up to 2 mm. long arising laterally or terminally from the column; anthers 4–5 mm. long by 0·5–1·0 mm. broad.

Text-fig. 3F; Pl. **1**, fig. F; Pl. **2**, fig. F; Pl. **3**, fig. C.

Exsiccata. *Balfour*, *Cuming* 1864 (Hb. Mus. Brit.); *Barkly* 1870, *Horne* 1875 (Hb. Kew); *V/3061*, Bassin Anglais, 17 January 1942; *V/3115*, Perrier, near the Mare-aux-Vacoas; *V/3116*, St Aubin, 10 July 1946 (Hb. Maur. Inst.); *F. 410* (Hb. Mus. Par.).

Distribution. Mauritius, endemic. Common in the uplands above 1200 ft.

P. eydouxia is the most widely spread of the Mauritius species, occurring usually in gregarious clumps of 5–10 or more trees on stream banks and in native thickets in regions of heavy rainfall. The large head with flat-topped, multilocular drupes readily distinguishes it from all other species.

10. **Pandanus glaucocephalus** Vaughan & Wiehe sp. nov.

Arbor valde ramosa vel frutex 6–8 m. altus, trunco 20 cm. diam. Folia 100–140 cm. longa, 6 cm. lata, apicem versus sensim attenuata ibique acuta, margine et costa dentibus brevibus pallidis fulvis armata. Syncarpium solitarium, globosum, 17–20 cm. diam., drupae 25–45 in syncarpio ad maturitatem glaucescenti, compressae vel irregulariter angulares, 12–20-loculares, 7–9 cm. longae, 8 cm. latae, 3 cm. crassae, in tertia superiori parte liberae; stigmata sessilia, reniformia, 2–3 mm. lata, rimis vel sulcis separata.

Low much-branched tree, 6–8 m. high. Stem up to 20 cm. diam. with slate-grey bark, stilt roots absent or few, confined to base of stem. Leaves 100–140 cm. long by 6 cm. wide, pale green, often waxy on both surfaces, gradually tapering to an acuminate apex; marginal spines very small, pale yellow or brown, lower surface of midrib spinous in the upper two-thirds. Female head globose, glaucous grey, 17–20 cm. diam. with 35–45 drupes, peduncle short, stout, the ultimate bract leaves overtopping the head. Drupes 12–20-locular, 7–9 cm. long by 8 cm. broad and 3 cm. deep, strongly compressed or irregularly hexagonal, free in the upper third or quarter, the free portion dome-shaped with a flat or slightly depressed apex. Stigmas scattered, flat, sessile, reniform, 2–3 mm. broad, separated by narrow fissures which extend down the exposed surface of drupe. Mesocarp fibrous, divided in the upper half by the woody endocarp which is 1·5–2·0 cm. thick. Male flower unknown.

Text-fig. 2F; Pl. **2**, fig. H; Pl. **4**, fig. C.

Exsiccata. *V/3017* type, near Le Pétrin 7 March 1942; *V/3017a*, near Plaine Champagne (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Occurs as isolated clumps in exposed situations on the plateau above 1800 ft. in the vicinity of Les Mares and Crown Land Le Pétrin.

This species has affinities with *P. barklyi* which it closely resembles in its vegetative characters. The dense crown of leaves frequently causes the lateral branches to break off, and growth is continued on the ground by means of adventitious roots. Germinating drupes and young plants have been observed in the neighbourhood of old trees.

11. **Pandanus carmichaelii** Vaughan & Wiehe sp. nov.

Arbor parva, vel frutex, trunco tenui et ramis decumbentibus, radicibus aereis paucibus. Folia 120 cm. longa, 7–8 cm. lata, sensim attenuata et acuminata, margine et costa distanter spinis fuscis armata. Syncarpium solitarium, 15 cm. diam., breviter pedunculatum, ad maturitatem rufescens; drupae 125–150 in syncarpio, 2–4-loculares, 4–4·5 cm. longae, 2 cm. latae, paullo compressae, cuneatae, 5–6-gonae, apice fere plano vertice areolato; stigmata magna, plana, 4–6 cm. lata. Spadices masculae 50–55 cm. longae, 8–12-spicatae, pendulae; spicae saepe 15 cm. longae. Stamina ad 3–8-fasciculata et ad spicam columnariam brevem disposita; filamenta 5–6 mm. longa; antherae 3 mm. longae.

Shrub or low tree forming a dense entangled thicket up to 4 m. high. Stems decumbent at first and then erect 8–10 cm. diam., reddish brown becoming grey on exposure with fissured flaky bark and occasional wart-like spines. Stilt roots few, 3–4 cm. diam., arising from all parts of the stem. Leaves 120 cm. long by 7–8 cm. broad, glaucous green, waxy on both surfaces, stiff and ascending, narrowing suddenly to an acute apex. Marginal spines yellow or dark brown. Pneumatophores present. Female head 15 cm. diam. spherical or trigonoglobose with 125–150 drupes immersed in the tristichous boat-shaped bracts. Drupes 2–4-locular, 4–4·5 cm. long by 2 cm. broad, scarcely compressed, cuneate, regularly 5–6-angled, united up to the flat-topped apex which has conspicuous corky fissures; joined portion bright red when ripe. Stigmas 4–6 cm. broad, flat, sessile, irregular or more or less reniform. Endocarp woody, 1–1·5 cm. thick, penetrated by the fibres of the mesocarp. Male spadix up to 55 cm. long, main rachis cylindrical bearing 8–12 lateral branches which are triangular in section and up to 15 cm. long. Basal bracts boat-shaped and keeled in the lower half, becoming linear and leaf-like upwards, 4·5 cm. long by 4 cm. broad; apical or terminal bracts 6–10 cm. long by 2 cm. broad. Stamens in groups of 3–8 with filaments joined at the base or united in the lower fifth or sixth; filaments 5–6 mm. long by 0·5 mm. broad, the anthers 3 mm. long with a mucronate apex.

Text-fig. 2H; Text-fig. 3C; Pl. **2**, fig. A.

Exsiccata. *V/3135, V/3187* (types), *V/3188*.

Distribution. Mauritius, endemic. It is known only from a single site at Le Pétrin in the uplands at an altitude of 2200 ft. where it forms a large elliptical-shaped thicket covering an area of about 250 square metres.

This new species is characterized by the spherical head with flat-topped scarcely protruding drupes, bearing rather large flat stigmas. Young plants or seedlings are not known, and attempts at germination have not been successful. We have dedicated this species to Captain Dugald Carmichael who was one of the first students of Mauritius pandans.

It seems very probable that this is Carmichael's *P. cauliflorus* of which he says: 'fruit sessile axillary nearly globular about 2 lb. in wt. and consisting of 100 drupes cuneiform from the very top and truncate with central depression in which is lodged a solitary stigma. The pulp of the fruit is scarlet. Grows on the bank of the Créole river.' Unfortunately he does not give a drawing, but with the exception of the unilocular drupe his description agrees very well with this species.

12. **P. macrostigma** Martelli in *Webbia*, **4**, 22, t. 41, f. 1–16 (1913) et loc. cit. **4**, 418 (1914).

Drupes 6–6·5 cm. long by 3·5–4 cm. broad and 2·5–3 cm. deep, 3–6-locular, slightly compressed, free in the upper sixth, joined portion acutely tapering towards the base, free portion dome-shaped or rounded and sometimes grooved or depressed between the raised apices of the carpels. Stigmas 5–8 mm. diam., fleshy, irregular or subreniform, somewhat oblique or pointed. Woody endocarp occupying the middle third of the fibrous mesocarp.

Exsiccata. Hb. Martelli, type (Bot. Mus. Fl.).

Distribution. Mauritius, endemic?

Martelli founded this species on some drupes collected by a missionary without any precise indication of locality and without information or description of its habit or vegetative characters. The drupes do not resemble any other known mascarene species. Owing to the paucity of material it is difficult to refer this species with certainty to any particular section of the genus. Two drupes in Martelli's herbarium, which we have had the opportunity of examining through the kindness of Dr R. Pichi-Sermolli, have fleshy, somewhat irregular stigmas not unlike those of the section *Keura*.

13. **P. spathulatus** Martelli in *Webbia*, **1**, 365 (1905) et loc. cit. **4**, 31, t. 23, figs. 1–4 (1913).

Drupes 2–3 (up to 10?) locular by 4–5 cm. broad and 2·5–3 cm. deep, compressed, 5–7-angled, with a flat apex or areole 1–2 cm. broad. Carpels uniseriate or scattered, stigmas 5 mm. (more rarely 3 mm.) diam., sessile, flat, cordate or reniform.

Text-fig. 2I.

Exsiccata. *Bouton*, 7 January 1865; Barkly No. 5, 2 November 1864 (Hb. Kew) *Cuming*, 1864; *Cutler* (Hb. Mus. Brit.); *Bouton*, F 4420 (Hb. Mus. Par.).

Distribution. Mauritius, endemic; also Réunion?

This species has not been found in the field by recent workers, and the drupes do not match any species known at the present time. Martelli based this plant on drupes in the Paris herbarium supposed to have been collected by Bouton in Réunion. Bouton's drupes in the Kew herbarium are without locality, and although Bouton made extensive collections in Mauritius it is not clear whether he ever collected in Réunion; the occurrence of this species in Réunion, therefore, cannot be confirmed. In the Kew Herbarium there are drupes collected in Mauritius by Sir Henry Barkly, unfortunately without precise locality. Our knowledge of *P. spathulatus* is thus very fragmentary, based as it is on dried fruits inadequately labelled as to exact sites. This species has close affinities both with *P. barklyi* and with *P. glaucocephalus*, and may prove to be merely a variety of the latter with fewer loculi and larger stigmas. In the British Museum Herbarium there is a probable form of *P. spathulatus* with as many as ten loculi and stigmas from 3 to 4 mm. broad, thus forming a connecting link between *P. glaucocephalus* and *P. spathulatus*. The relation of these species, however, can only be decided by an examination of the plants in the field.

14. **P. incertus** Vaughan & Wiehe sp. nov.

Arbor parva, vel frutex, trunco 10–12 cm. diam. paullo verrucoso basi decumbenti. Folia 80–100 cm. longa, 5·5–6·0 cm. lata, sensim longe attenuato-acuminata. Syncarpium solitarium, clavatum vel subglobosum, pedunculo brevi; drupae 100–125 in syncarpio, 1–4-loculares, 45 cm. longae, 3 cm. latae, 1·5 cm. crassae, distincte compressae, in quinta superiori parte liberae; loculi 1-seriatim vel irregulariter dispositi, apice breviter convexo-pyramidali; stigmata sessilia, plana, magna, reniformia, 5–8 mm. lata. Endocarpium osseum, 1–1·5 cm. spissum.

A low tree, 2–3 m. high, the trunk 10–12 cm. diam., decumbent at first then ascending with pale reddish grey bark armed with blunt wart-like spines. Stilt roots few, 2–3 cm. diam., confined to base of stem. Leaves 80–100 cm. long by 5·5–6·0 cm. broad, reduplicate, narrowing gradually to the channelled acute apex. Female head spherical or club-shaped, 16 cm. diam. with 100–125 drupes, clasped by the tristichous persistent bract leaves. Drupes 1–4-locular, carpels uniseriate or irregular, 4–5 cm. long by 3 cm. broad and 1·5 cm. deep, compressed, free in the upper fifth, free portion dome-shaped with deep corky fissures, joined portion orange-red when ripe. Stigmas 5–8 mm. broad, reniform or irregularly cordate. Endocarp densely woody 1–1·5 cm. thick penetrated by the pale yellow fibres of the mesocarp. Male flowers unknown.

Text-fig. 2J; Pl. 4, fig. F.

EXSICCATA. *V/3202* (type) (Hb. Maur. Inst.).

DISTRIBUTION. Mauritius, endemic.

Although known from a single individual found on the upland plateau near Chemin Mingot, the club-shaped syncarp and large stigmas indicate its distinctness from other known species. It approaches in some respects *P. spathulatus*, but a critical comparison in the field between these two species would be necessary to establish their relationships.

15. **P. heterocarpus** Balf. f. in Baker, *F.M.S.* 399 (1877) et in *Philos. Trans.* **168**, 378 (1879); Warburg in *Pflanzenr.* Pand. 58 (1900); Martelli in *Webbia*, **4**, 16 (1913). *P. tenuifolius* Balf. f. loc. cit. 380; Warburg, loc. cit. 58.

'Gros vacoa', 'Vacoa Chevron', 'Vacoa cale rouge', 'Vacoa parasol'.

Much branched low tree 6–7 m. high, often forming an umbrella-like crown. Main stem 12–18 cm. diam., with a dark brown bark armed with short, wart-like spines; branches ending in fan-like tufts of leaves. Leaves 50–100 cm. long by 4–6 cm. broad, narrowing gradually upwards from the amplexicaul base, the margins and under surface of midrib armed with orange or red spines. Female head 10–18 cm. diam. globose or elliptical-oblong with 30–75 drupes. Drupes 2–5-locular, 4–5 cm. long by 3–4 cm. broad, carpels scattered, 5–6-angular, slightly compressed, joined nearly to the top, the exposed portion flat or convex or somewhat dome-shaped, dark green or purple when ripe and often with a distinct red border at the base. Stigmas 2–6, sessile, reniform, 3–4 mm. wide, inserted on a flat or slightly depressed oval areole 1–1·5 cm. broad which has a distinct corky margin. Male spadix 30–35 cm. long, bearing 12–15 lateral branches or spikes. Bract leaves boat-shaped or keeled at the base with spinous margins contracting suddenly into a narrow acuminate apex. Stamens 5–10, with filaments united to form a staminal column 4–5 mm. long; free portion of filaments up to 1–2 mm. long.

Text-fig. 1A, B.

EXSICCATA. *Balfour* (Hb. Kew); *V/3181* (Hb. Maur. Inst.).

DISTRIBUTION. Rodriguez, endemic. This species is still very common on the island and imparts a distinctive physiognomy to the landscape.

As the specific epithet suggests, this species is extremely variable, not only in the size of the female head and the number and shape of the drupes, but also in its vegetative forms which vary considerably according to habitat. After examining a large number of plants in the field, in addition to fresh and dried material of drupes, we agree with Martelli that *P. tenuifolius* Balf. f. cannot be maintained as a separate species. One of the principal distinctions made by Balfour was that *P. tenuifolius* has fewer and more exserted drupes, characters which are found to be extremely variable in other species examined. Two different forms of drupe are shown in Text-fig. 1A and B. Moreover, similar female heads have been found on plants having the differing vegetative features used by Balfour to separate the two species. Balfour, himself, says in this connexion that 'certain trees on the island seem to possess characters intermediate between these species and may be hybrids'.

16. **P. pyramidalis** Barkly ex Balf. f. in Baker, *F.M.S.* 399 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 60 (1878); Warburg in *Pflanzenr.* Pand. 60, fig. 16, D–E (1900); Martelli in *Webbia*, **4**, 28 (1913).

A tree reaching 12–15 m., freely branching in whorls of two to four, the branches more or less horizontal and ending in drooping tufts of leaves. Stem erect, or slightly decumbent at the base, 20 cm. diam., bark greyish brown with copious short wart-like spines; stilt roots crowded at base of stem. Leaves 100–150 cm. long by 4–6 cm. broad, gradually tapering from the middle to an acute apex, marginal spines very small and close set, brownish yellow, becoming black-tipped. Female head globose, somewhat depressed or flattened, 15 cm. diam., with 100–150 drupes and a strongly recurved or twisted peduncle with leaf-like bracts overtopping the head. Drupes 2–6-locular, carpels usually scattered, rarely uniseriate, compressed, 5–6 cm. long by 3–4 cm. broad and 2–3 cm. deep, free in the upper fifth or sixth, the free portion dome-shaped, bright green with conspicuous corky fissures; joined portion angular lemon-yellow when ripe. Stigmas flat, reniform, 2–3 mm. broad, scattered over an oval-shaped often depressed areole. Male flower unknown.

Text-fig. 2K; Pl. **1**, fig. B; Pl. **4**, fig. E.

Exsiccata. *Cuming*, 1864 (Hb. Mus. Brit.); *Bouton*, 1864, *Horne*, 1875, *Balfour*, 1875, *Barkly* (Hb. Kew); *V/3178, V/3179*, Grotte Bonnefin Curepipe 1 March 1947 (Hb. Maur. Inst.).

Distribution. Mauritius, endemic.

A very rare species. The only living plants known comprise a small stand of eight trees at Grotte Bonnefin near Curepipe, and a solitary plant in the river reserves near La Marie water-works. No germinating seeds or young plants have been found, and attempts at germination have been unsuccessful. The dried drupes usually found in herbaria are very similar to the larger forms of *P. barklyi.*

17. **P. barklyi** Balf. f. in Baker, *F.M.S.* 397 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 42 (1878); Warburg *Pflanzenr.* Pand. 62, fig. 16, U–V (1900); Martelli in *Webbia*, **4**, 7 (1913). *P. sylvestris* Kurz in *J. Asiat. Soc. Beng.* **38**, 2, 3, 149 (1869) et in *Flora Bot. Z.* **52**, 453 (1869); non Bory. *Vinsonia sylvestris* Gaudich. *Bot. Voy. Bonite*, t. 17, figs. 16, 17 (1841); Walp. *Ann.* **1**, 756 (1848); Ad. Br. in *Ann. Sci. Nat.* (6), **1**, 290 (1875).

A shrub or low tree reaching 4–5 m., freely branching from the base upwards. Main stem decumbent at first, then erect, 10–18 cm. diam., with pale grey fissured bark armed with blunt warty spines; stilt roots 3–4 cm. diam., few, confined to base of stem. Leaves 100–150 cm. long by 6–7 cm. broad, dark green with a pale yellow translucent midrib, young leaves stiff and erect, later becoming bent sharply and drooping. Upper portion of stem clothed with a dense shag of rotting leaf bases; marginal spines minute, yellow-green, usually absent near base of leaf. Female heads very variable in size, 9–15 cm. diam., rarely 18 cm., more or less globose, bearing 50–100 drupes; peduncle 20–40 cm. long, trigonous, the bract leaves deciduous and not over-topping the head. Drupes 2–5- (rarely 8-) locular, typically uniseriate, more rarely with scattered carpels, very variable in size and shape, free in the upper third or quarter, 3·5–6 cm. long by 2·5–5 cm. broad and 0·8–3 cm. deep, compressed, somewhat angular or ribbed. Free portion pyramidal, dome-shaped, or truncate, olive-green, brown, or purple when ripe; apex either slightly concave or depressed, and sometimes areolate or truncate with stigmas divided by corky fissures. Stigmas flat, irregular or reniform, 3–4 mm. diam. Male spadix very variable in size, 20–60 cm. long. Main rachis flattened or elliptical, 1·5 cm. broad, bearing 10–12 lateral trigonous spikes or branches 8–12 cm. long. Bracts greenish white or white, boat-shaped, keeled below and narrowing suddenly in the upper two-thirds to a sharp acuminate apex, basal bracts up to 80 cm. long, becoming progressively shorter, the apical bracts less than 6 cm. long, staminal column with marked fasciation, 0·8 cm. long, elliptical or oblong in section, bearing 15–21 terminal or rarely lateral stamens 2–3 mm. long with short free filaments. Abortive ovaries sometimes present at the top of the staminal column.

Text-fig. 1E (fissured drupes from small head); Text-fig. 1G (typical drupes from large head); Text-fig. 3H (stamens); Pl. **2**, fig. J (large head); Pl. **2**, fig. K (small head with fissured drupes); Pl. **3**, figs. B, D (male spadix); Pl. **4**, fig. H (young syncarp); Pl. **3**, fig. E (abortive ovary).

Exsiccata. (i) Form with large head; Barkly No. 6, *Horne* 1875 (Hb. Kew); *Cuming* 'A', abnormally shaped drupes from base of head, *Cuming* 'B' (Hb. Mus. Brit.); *V/3178* (Hb. Maur. Inst.).

(ii) Form with small head and fissured truncate drupes; *Barkly* No. 11 (Hb. Kew); *V/3016* (Hb. Maur. Inst.).

(iii) Form with small head and dome-shaped drupes; *V/3801* (Hb. Maur. Inst.).

(iv) Male plants; *V/3112*A, *V/3154* (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Common in the uplands, particularly in the marshy indigenous vegetation near Midlands, Les Mares, Le Pétrin, and hills overlooking the Black River Gorges, usually in open situations where it forms large thickets or gregarious clumps.

This species plays an interesting part in the transitional stages of the sere from marshland to indigenous thickets. The lateral branches often become top-heavy and break off, growth continuing on the ground by means of adventitious roots; by this means large irregular or more or less circular thickets are formed dying away in the interior where other native species are able to grow on the drier soil produced.

The female head and drupes of this species are extremely variable and, owing to very inadequate herbarium material, it has been a source of great perplexity to systematists. The examination of some scores of male and female plants in the field indicates that it is not feasible at this stage to segregate the numerous forms which occur into definite subspecies or varieties, as many intermediate and connecting types may be found; only one of them, described below, seems to deserve varietal rank. Rather than burden the literature by creating a number of names for varieties whose relationships are by no means clear, it will suffice here to indicate the principal forms of the *P. barklyi* complex to serve as a future working basis. In his original descriptions of *P. barklyi* Balfour refers to the 'apex of the drupe a transversely elongated ridge deeply cleft between the prominent stigmas' (Pl. **2**, fig. K), and this is the form illustrated by Gaudichaud in his Atlas under the name of *Vinsonia sylvestris*; it usually has a small syncarp often not exceeding 10 cm. in diameter on a long slender peduncle with small drupes 3–4 cm. long. Another type has a very large female head which may be as much as 18 cm. diam. with dome-shaped drupes up to 6 cm. long (Pl. **2**, fig. J). Other forms have small syncarps with 40–80 dome-shaped drupes not exceeding 3–4 cm. All the male flowers examined seem to vary only in size, the older more robust trees giving rise to large male spadices which may be as much as 60 cm. long.

17*a*. **P. barklyi** var. *macrocarpus* Vaughan & Wiehe var. nov.

Syncarpium globosum, 10–12 cm. diam.; drupae compressae, glaucae, 30–40 in syncarpio, 5 cm. longae, 4–5 cm. latae, 2 cm. crassae, 4–6-loculares, uniseriatae, ad medium liberae, vertice inter stigmata fisso. Endocarpium osseum, in dimidia superiori parte druparum locatum, vix 1 cm. spissum.

Female head globose, glaucous-grey, 10–12 cm. diam. comprising 30–40 drupes. Drupes 4–6-locular, uniseriate, free in the upper third or half, strongly compressed, 5 cm. long by 4–5 cm. broad and 2 cm. deep. Stigmas flat, reniform, 2–3 mm. broad, often separated by corky fissures; endocarp narrow, woody, less than 1 cm. thick bisecting the upper half of the fibrous mesocarp.

Text-fig. 1F.

Exsiccata. S. Pelte (type) (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Marshy ground at Gaulette Sérée, near Camp Thorel.

Differs from other forms of *P. barklyi* in its smaller head with large, much exserted, drupes which are often as broad as long. The structure of the drupe suggests affinity with the new species *P. glaucocephalus*.

18. **P. iceryi** Horne ex Balf. f. in Baker, *F.M.S.* 400 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 49 (1878); Warburg in *Pflanzenr.* Pand. 60 (1900); Martelli in *Webbia*, **4**, 17 (1913).

A tree up to 10 m. high with an unbranched stem terminating in an erect tuft of leaves. Leaves 80–200 cm. long by 7·5–15 cm. broad, narrowed suddenly to the apex, bright green above, glaucous beneath the margins, armed except at the middle with closely set white spines; blade reduplicate on each side of the midrib with a tendency to split at the top. Female head ovoid, 8–10 cm. long, containing about 40 drupes, the peduncle arising from the main trunk, under a foot long, with numerous small leafy bracts. Drupes 2–5-locular, 3·5 cm. long by 1·5–2 cm. broad, free in the upper third, slightly compressed, regularly 5–6-angular, apex dome-shaped, stigmas prominent, flat, sessile, reniform, 3 mm. broad. (Horne.)

Pl. 4, fig. B.

Exsiccata. *Horne* (Hb. Kew).

Distribution. Mauritius, endemic. 'In forests between the Piton du Milieu and Cent Gaulettes Mt. also near Fressanges' (Horne).

John Horne's specimen, preserved in the Kew Museum, is probably the type of this species; we have not been able to trace the original manuscript of Horne, and the above description is adapted from that given by Balfour in Baker's *Flora*. We have not seen *P. iceryi* in the field, but the dried drupes of this species can hardly be distinguished from those derived from the small syncarps of *P. barklyi* with dome-shaped drupes, though fresh material might reveal significant differences. There would be little hesitation in regarding *P. iceryi* as a variety of *P. barklyi* were it not for the very curious arrangement of the female heads which are borne on drooping, densely clustered, spirally disposed peduncles arising from the main trunk (Pl. 4, fig. B). This particular specimen may be an aberrant form due to injury or some other cause, but Horne gives several localities in which it has been found and has referred to its strange behaviour in his description. It would indeed be remarkable if a pandan produced a genuine cauliflorous inflorescence, and it may be that these syncarps are produced from the terminal buds of abortive shoots which occur occasionally in other species near the apex of the main stem.

19. **P. utilis** Bory, *Voy.* **2**, 3 (1804); Bojer, *H.M.* 301 (1837); Balf. f. in Baker, *F.M.S.* 398 (1877) et in *J. Linn. Soc.* (*Bot.*), **17**, 63 (1878); Cordem. *Fl. Réunion*, **139** (1895); Warburg in *Pflanzenr.* Pand. 61 (1900).

'Vacoa.'

An erect tree, 15–20 m. high, freely branching, the ultimate branches ending in ascending tufts of leaves. Leaves 75–200 cm. long by 6–10 cm. broad, the reddish margins armed with red spines. Female heads very variable in shape and size, up to 20 cm. diam., drooping, trigono-globose, depressed or cylindrical. Drupes 100–200, 4–8-locular, 3–3·5 cm. long by 2·5–4·0 cm. wide and 1·5–2·0 cm. deep, compressed, dome-shaped, free in the upper half, the free portion deep shining green with a purple or red band at the base; joined portion not tapering, truncate at the base which is 2–3 cm. wide. Stigmas flat, reniform, irregular, the apex of the drupe often cleft between the stigmas which are 1·5–2·0 mm. broad. Male spadix 50–80 cm. long. Stamens borne in groups of 6–10 at the end of slender columns 10–12 mm. long; free portion of filaments 5–6 mm. long. Anthers 5 mm. long by 0·75 mm. broad, apex acute or acuminate.

Text-fig. 3I.

Exsiccata. *Balfour*, *Barkly* (Hb. Kew), *Gaudichaud*, *Richard*, *Pervillé*, *Daruty* (Hb. Mus. Par.); *V/3151* (Hb. Maur. Inst.).

Distribution. Madagascar, extensively cultivated in the Mascarene Islands. Cordemoy inclines to the view that *P. utilis* is indigenous in Réunion.

This species is very common everywhere and more or less naturalized. The leaves were formerly used for sugar bags and are still widely employed for making baskets and mats. The ends of the stilt roots are often made into rough brushes for whitewashing. Bouton (1857) records the use of decoctions of these roots in the treatment of venereal disease, while Daruty (1886) refers to their aphrodisiac properties, no doubt an example of sympathetic magic.

20. **P. purpurascens** Thouars in *Bull. Sci. Soc. Phil., Paris*, **183** (1808) et in Desv. *J. Bot.*, **1**, 44 (1808); Lam. *Encycl. Bot.*, Suppl., **1**, 576 (1810); Spreng. *Syst. Veg.* **3**, 898 (1826); Bojer, *H.M.* 302 (1837) (hab. excl.); Kunth, *Enum. Pl.* **3**, 97 (1841) (hab. excl.); Kurz in Seem. *J. Bot., Lond.*, **5**, 133 (1867) (hab. excl.); Warburg in *Pflanzenr.* Pand. 60 (1900); Martelli in *Webbia*, **4**, 28 (1913).

'Baquois à semences purpurines' (Lamarck), 'Vacoua marron rouge'.

Shrub 2–3 m. high. Leaves 60–70 cm. long by 7–8 cm. broad, smooth, flexible, strongly reduplicate, narrowing suddenly at the apex to a blunt or obtuse tip. Female head 7–10 cm. diam., drupes purple or red, 1–4-locular, 3–4 cm. long by 2–2·5 cm. broad, not strongly compressed, more or less ribbed. Stigmas reniform, flat, sessile, 2–2·5 mm. broad, placed close together at the apex of the dome-shaped drupes which are free in the upper third or half.

Text-fig. 1I.

Exsiccata. Gaudichaud F 492 (Hb. Mus. Par.).

Distribution. Réunion, endemic. Rampes Le Tort (Cordemoy). Partie basse de la Plaine des Palmistes vers le Pont Payet (P. Rivals).

Easily recognized, according to Cordemoy, by the conspicuous reddish purple colour of the ripe female head. Though distinct from any Mauritius species it has affinities with some forms of *P. barklyi*.

21. **P. sylvestris** Bory, Voy. 2, 260 (1804); Balf. f. in *J. Linn. Soc.* (*Bot.*), **17**, 62 (1878); Warburg in *Pflanzenr.* Pand. 60, fig. 16K (1900); Martelli in *Webbia*, 4, 32 (1913). *P. nemorosus* Cordem. *Fl. Réunion*, **140** (1895). *P. elegans* Thou. in *Bull. Soc. Phil., Paris*, **184** (1808); Cordem. loc. cit. 141 (1895). *P. humilis* Jacq. *Fragm.* 21, t. 14, fig. 2 (1809). *Vinsonia elegans* Gaudich. *Bot. Voy. Bonite*, t. 17, figs. 12, 13 (1841). *V. humilis* Gaudich. loc. cit. t. 17, figs. 10, 11. *V. lucida* Gaudich. loc. cit. t. 17, figs. 14, 15.

Small tree, 3–4 m. high, branching freely. Leaves 40–80 cm. long by 2–3 cm. broad, the midrib and margin armed with closely set short red spines. Female head globose or somewhat oblong, 6–7 cm. diam., borne at the end of a long peduncle. Drupes 20–30, 2 cm. long by 1·5–2 cm. broad, free in the upper half or two-thirds, 2–6-locular, angular and broadly truncate at the base, the free portion pyramidal narrowing abruptly to the apex which is often cleft between the stigmas. Stigmas small, reniform, 1–1·5 mm. broad.

Text-fig. 1H.

Exsiccata. *Delessert*, F. 493, F. 489 (Hb. Mus. Par.).

Distribution. Réunion, endemic. Bois Blanc and Piton de Crac (Bory); dans les environs de la Plaine d'Affouches près de l'Ilette à Guillaume (P. Rivals).

P. elegans Thou. (*Vinsonia elegans* Gaudich.) which Cordemoy considers a good species is one of the many forms of this extremely variable plant. Balfour assigns *P. elegans* to this species and not, as Cordemoy erroneously states, to *P. montanus*.

22. **Pandanus obsoletus** Vaughan & Wiehe sp. nov.

Arbor parva, 5 m. alta, trunco inferne radicibus aereis fulto; folia 100–125 cm. longa, 5–6 cm. lata, margine et costa distanter rubro-spinosis. Syncarpium solitarium, longe pedunculatum, pendulum, depresso-globosum. Drupae 250–350 in syncarpio, 1–3-loculares, 4–5 cm. longae, 1·5–2·5 cm. latae, quinta superiori parte liberae, pyramidatae, basi annulo purpureo cinctae, vertice haud areolato, angusto, inter stigmata fisso; stigmata plana, sessilia, 2–3 mm. lata.

A low tree not exceeding 5 m., with paired or ternate branches. Stem decumbent at the base then erect, 15–17 cm. diam.; bark pale fawn, with conspicuous reddish brown leaf scars, sparsely armed with wart-like blunt spines and clothed with irregular bands of papery leaf-bases. Stilt roots 3–4 cm. diam., confined to decumbent portion of stem. Leaves 100–125 cm. long by 5–6 cm. broad, stiff, pale green above, glaucous and waxy below, tapering gradually to a slender acuminate apex; leaf-bases red-ochre, marginal spines red, widely spaced, the lower surface of midrib with spines in upper third. Syncarp pendulous, globose or trigonous, depressed at the apex, up to 17 cm. diam. with 250–350 drupes, peduncle reflexed or arcuate 40–50 cm. long, the bract leaves overtopping but not clasping the syncarp. Drupes 1–3-locular, uniseriate, slightly compressed, 4–5 cm. long by 1·5–2·5 cm. broad, free in the upper fifth, the free portion dome-shaped or pyramidal, faintly ribbed, dark green with a deep red or purple ring at the base, joined portion angular, red when ripe. Stigmas flat, irregular, 2–3 mm. broad. Male flowers unknown.

Text-fig. 2A; Pl. **4**, fig. A.

Exsiccata. *V/3131* (type), Le Pétrin 24 November 1946 (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Le Pétrin near Forest Station, 2100 ft.

The dried drupes have a superficial resemblance to those of *P. prostratus*; the two species, however, are quite distinct and differ widely in habit and growth form; the true affinities of this species are with *P. utilis* and *P. vandermeerschii*. The unique individual from which this species was described has recently succumbed to a fungal attack, probably due to a species of *Phytophthora*.

23. **P. prostratus** Balf. f. in *J. Linn. Soc.* (*Bot.*), **17**, 59 (1878); Warburg in *Pflanzenr.* Pand. 62 (1900); Martelli in *Webbia*, **4**, 28, t. 25, f. 9–12 (1913). *P. conoideus* Thouars in *Bull. Sci. Soc. Phil., Paris,* **185** (1808) et in Desv. *J. Bot., Paris,* **1**, 47 (1808); Poir in Lam. *Encycl. Bot.*, Suppl., **1**, 577 (1808); Kunth, *Enum. Pl.* 3, 97 (1841); Kurz, in Seem. *J. Bot., Lond.*, **5**, 130 (1867) et in *J. Asiat. Soc. Beng.* **38**, 3, 150 (1869) (excl. syn.) et in *Flora Bot. Z.* **3**, 454 (1869) (excl. syn.); Balf. f. in Baker, *F.M.S.* 398 (1877); non Lam.

'Baquois conique' (Lamarck), 'Vacoa marron'.

A much branched shrub or low tree 3–4 m. high with slender ascending branches forming a compact crown. Stem decumbent, then erect with dark brown or greyish bark, abundant warty spines and the persistent remnants of the leaf bases forming a dense shag beneath the apical tuft of leaves. Leaves 115–145 cm. long by 6 cm. broad, somewhat thin and drooping, narrowing gradually to an acute apex. Marginal spines white and crowded towards upper part of leaf, becoming black-tipped and scattered below. Female head globose, cylindrical or ob-ovaliform, erect at first then drooping, 17 cm. long by 15 cm. broad, with 300–350 drupes, peduncle up to 50 cm. long with leaf-like bracts overlapping but not clasping the head. Drupes 1–3-locular, uniseriate, compressed, 5 cm. long by 2 cm. broad and 1·5 cm. deep, free in the upper fifth, the free portion pyramidal or conical, ribbed, pale glaucous green, the joined portion lemon-yellow when ripe. Stigmas flat, irregular, 2–3 mm. diam. Male spadix 75–95 cm. long, the male rachis flattened up to 1 cm. wide, slender drooping, bearing 8–14 cylindrical lateral branches or spikes up to 25 cm. long. Bract leaves greenish white, deciduous, 5–7·5 cm. long, becoming progressively smaller towards apex of inflorescence. Staminal column short, elliptical, 2 mm. long with 6–8 stamens formed by the fasciation of the lower portion of the filaments, the free portion of which is 5 mm. long. Anthers 3–5 mm. long by 0·75 mm. broad.

Text-fig. 2B; Text-fig. 3B; Pl. **2**, fig. L; Pl. **3**, fig. H.

Exsiccata. *Barkly* nos. 3 and 12, *Horne* no. 2, 1875, *Balfour* 1875 (Hb. Kew); *Daruty* F. 4279 (Hb. Mus. Par.); *V/3057* Curepipe (Hb. Maur. Inst.).

Distribution. Mauritius, endemic. Stream banks and native thickets in the uplands. Scattered individuals are fairly common and frequently found growing in association with *P. eydouxia*.

This species has a tendency to form compound female heads, and inflorescences are sometimes found with a smaller secondary head attached to the main peduncle.

Cultivated species

P. utilis is now very common throughout the Mascarenes; it is more or less naturalized, and it is therefore included for convenience of identification in the key and descriptions of the native species.

P. tectorius, belonging to the section *Keura*, has been recorded from Mauritius and Rodriguez, but we have not seen specimens. It is an extremely variable species, very common in the Indo-Pacific region, and may be readily distinguished by its large syncarp with 50–90, 6–12-locular, drupes which are 6–10 cm. long with the free apices crowned by the oblique, often mucronate, stigmas.

Several other ornamental species of doubtful identity have been introduced.

Doubtful or rejected species

P. delessertii (Gaudich.). Warburg in *Pflanzenr.* Pand. 55 (1900). *Eydouxia delessertii* Gaudich. *Bot. Voy. Bonite*, t. 18, figs. 7–8 (1841).

Warburg states that this species is a native of Réunion, but it is known only from the drawing in Gaudichaud's Atlas. Martelli believes it is nothing more than a form of *P. tectorius* but Martelli's illustrations of *P. tectorius* are very different from the species figured by Gaudichaud. No drupes remotely resembling this species have been found in the field or in collections examined.

P. madagascariensis (Gaudich.). Balfour f. in *J. Linn. Soc.* (*Bot.*), **17**, 52 (1878); Warburg in *Pflanzenr.* Pand. 58 (1900). *Dorystigma madagascariense* Gaudich. *Bot. Voy. Bonite*, t. 31, figs. 12–18 (1841).

Balfour suggests that this may be merely a small form of *Dorystigma mauritianum* Gaudich. Warburg maintains it with the habitat Madagascar; it is not known in the Mascarene Islands.

P. mauritianus (Gaudich.). Warburg in *Pflanzenr.* Pand. 58 (1900); Martelli in *Webbia*, **4**, 23 (1913); *Dorystigma mauritianum* Gaudich. *Bot. Voy. Bonite*, t. 13, figs. 25–27 (1841).

This species is based solely on the drawing in Gaudichaud's Atlas. It has already been noted that individual drupes exhibit great variation even in the same head and the creation of a new species on such slender evidence is hardly justified, especially in the absence of any authentic specimens. If Gaudichaud's drawing was made from fresh material there is some foundation for Balfour's suggestion that these drupes belong to *P. conglomeratus*.

P. ensifolius Thou. in *Bull. Soc. Phil., Paris*, **4** (1808) et in Desv. *J. Bot., Paris*, **1**, 46 (1808); Warburg in *Pflanzenr.* Pand. 65 (1900).

Attributed to Mauritius by Bojer; it is a Madagascar species.

P. reflexus (De Vriese), C. Koch, *Wochenschrift*, 132 (1858) nec Lodd.; Balf. f. in *J. Linn. Soc.* (*Bot.*), **17**, 60 (1878); Warburg in *Pflanzenr.* Pand. 57, fig. 17M–N (1900); Martelli in *Webbia*, **4**, 29 (1913); *Doornia reflexa* De Vriese in Hook. *Kew J.* **6**, 266 (1854).

A note in Warburg's monograph assigns this species to the East African Islands, possibly Réunion, but it is not mentioned by Cordemoy. Further reference has been made to this species in the note following *P. conglomeratus*.

P. multispicatus Balf. in Baker, *F.M.S.* 403 (1877); Martelli in *Webbia*, **4**, 24 (1913).

It has not been possible to confirm Martelli's statement that this species occurs in Réunion; it is probably endemic in the Seychelles.

P. lindenii Warburg in *Pflanzenr.* Pand. 88 (1900).

There is no evidence to support Linden's statement that this species, known only in the sterile state, came from Rodriguez.

We have no knowledge of the occurrence in the Mascarene Islands of the following species which are either nomina nuda or known only in the sterile state: *P. bromeliaefolius* Hort. Lodd. ex Desf. *Cat. Hort., Paris*, ed. 3, 9 (1829), *P. hoffa* Chap. MSS. Bojer, *H.M.* 303 (1837), *P. marginatus* Roxb. *Hort. Beng.* **71** (1814), *P. sessilis* Bojer, *H.M.* 302 (1837), and *P. vittariifolius* Bojer, *H.M.* 302 (1837).

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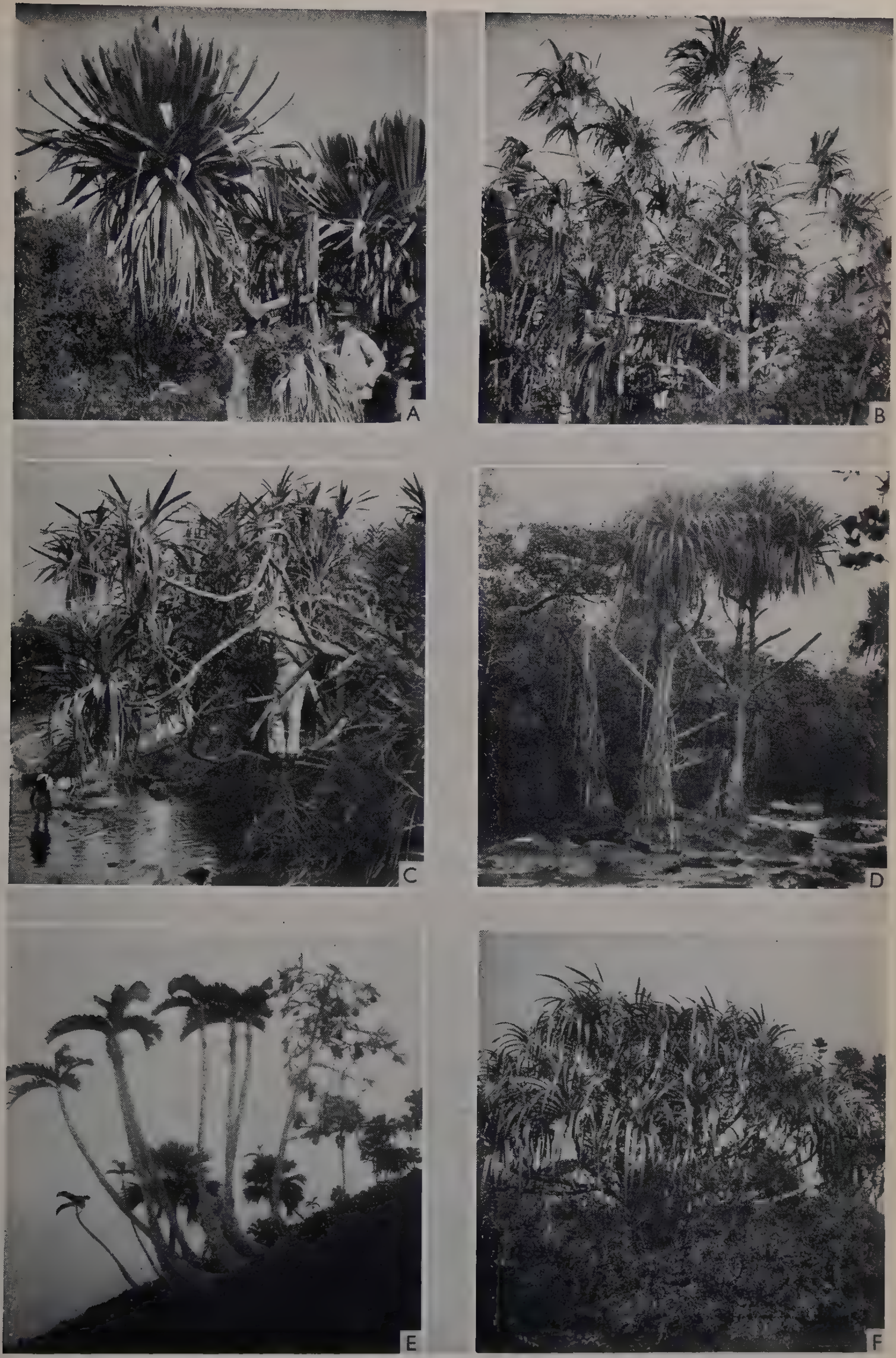
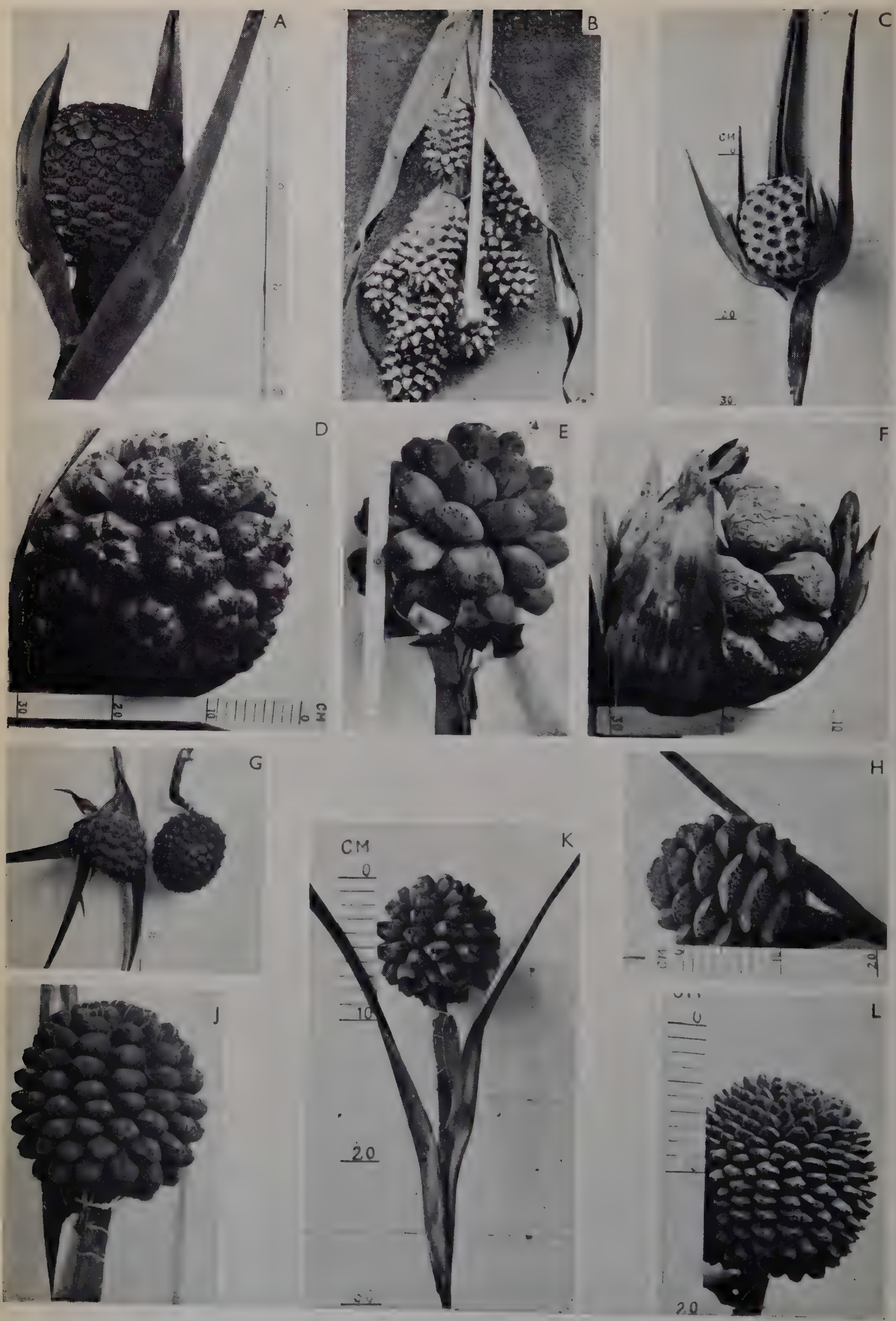


Pandanus spp.



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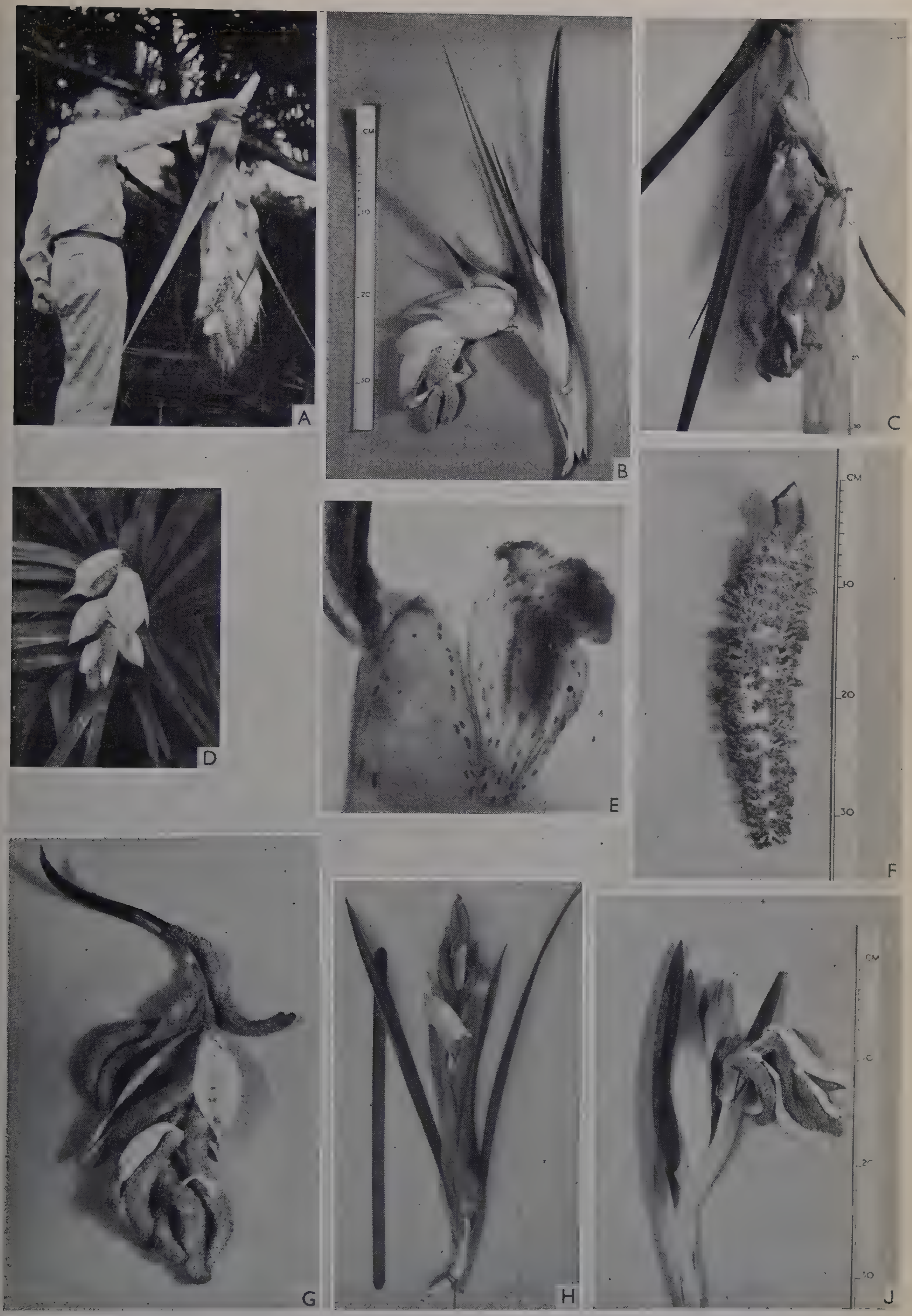

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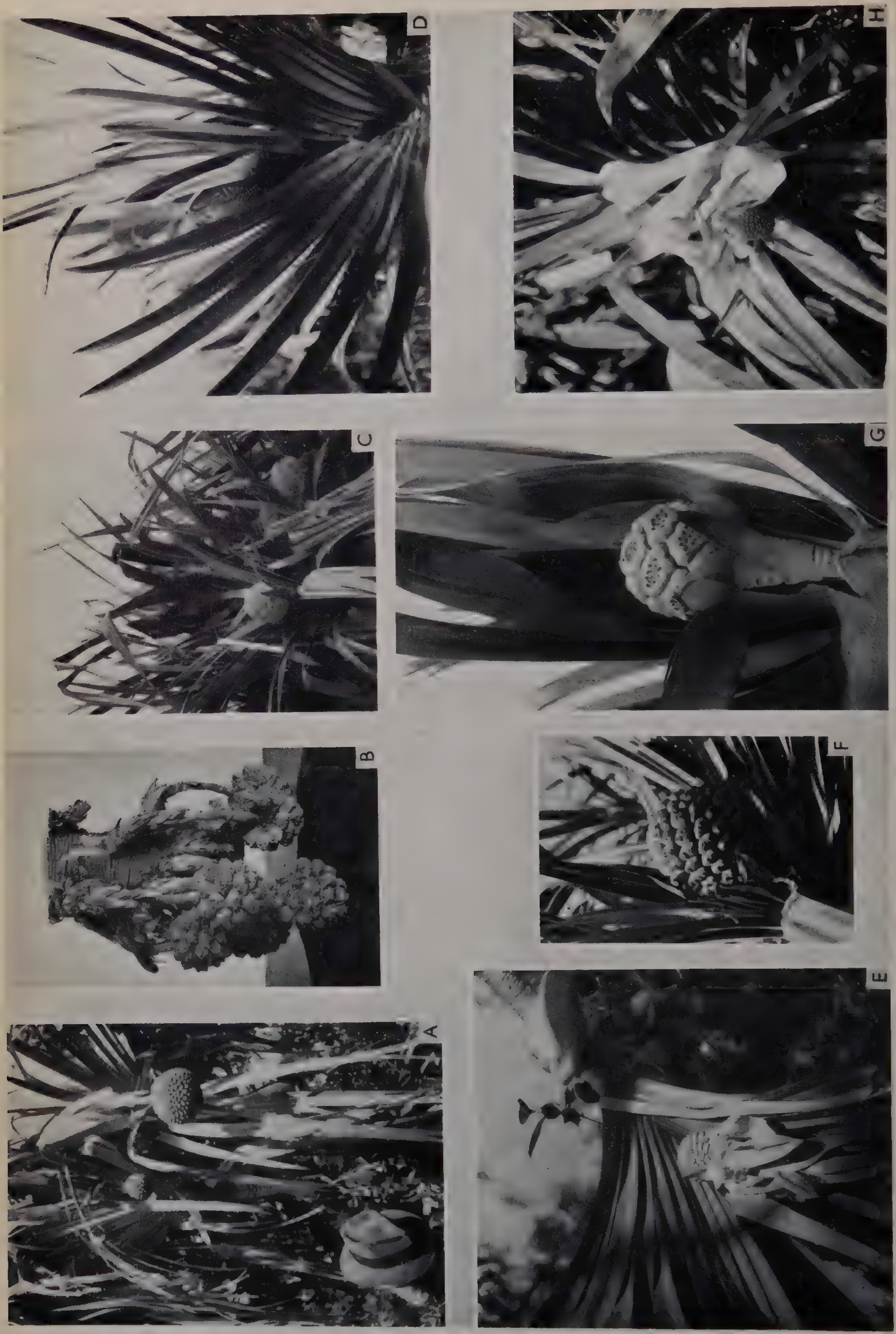

Pandanus spp.

EXPLANATION OF PLATES

PLATE 1

Fig. A. *P. drupaceus*. Midlands, Mauritius. Fig. B. *P. pyramidalis*. Curepipe, Mauritius. Fig. C. *P. sphaeroideus*. Cluny, Mauritius. Fig. D. *P. palustris*. Rivière du Poste, near Grand Bassin, Mauritius. Fig. E. *P. vandermeerschii*. Round Island, Mauritius, growing in association with endemic palms. Fig. F. *P. eydouxia*. Near Curepipe, Mauritius.

PLATE 2. Female heads or syncarps

Fig. A. *P. carmichaelii*. Fig. B. *P. conglomeratus*. From an old photograph; length of measuring tape 45 cm. Fig. C. *P. sphaeroideus*. Fig. D. *P. palustris*. Fig. E. *P. drupaceus*. Fig. F. *P. eydouxia*. Fig. G. *P. microcarpus*. Fig. H. *P. glaucocephalus*. Fig. J. *P. barklyi*. Form with large head and dome-shaped drupes. Fig. K. *P. barklyi*. Form with small head and fissured drupes. Fig. L. *P. prostratus*.

PLATE 3. Male inflorescences

Fig. A. *P. palustris*. Fig. B. *P. barklyi*. Fig. C. *P. eydouxia*. Fig. D. *P. barklyi*. Male spadix *in situ*, note conspicuous bract leaves. Fig. E. *P. barklyi*. Vertical section through staminal column showing abortive ovary. Fig. F. *P. palustris*. Lateral branch of spadix. Fig. G. *P. sphaeroideus*. Upper bracts removed, total length 40 cm. Fig. H. *P. prostratus*. Length of scale 50 cm. Fig. J. *P. rigidifolius*.

PLATE 4

Fig. A. *P. obsoletus*. Mature and young female heads. Fig. B. *P. iceryi*. The type specimen preserved in the Kew Museum (photo. F. Ballard). Fig. C. *P. glaucocephalus*. Three mature female heads. Fig. D. *P. rigidifolius*. A dwarf species with female head emerging from bracts, note three-ranked arrangement of leaves. Fig. E. *P. pyramidalis*. The fleshy bracts are pulled down to show female 'flower'; the peduncle twists round through an angle of 180° as it emerges from the crown of leaves. Fig. F. *P. incertus*. Mature female head showing large flat stigmas. Fig. G. *P. drupaceus*. Young female head, bracts near camera removed. Fig. H. *P. barklyi*. Female 'flower' surrounded by white fleshy bracts.

South African parasitic Florideae and their hosts. 1. Four members of the Rhodomelaceae which act as hosts for parasitic Florideae. By Mary A. Pocock, Ph.D, F.L.S.[1]

(With Plates 5–9 and 9 Text-figures)

[Read 5 February 1953]

The study of South African seaweeds has in the past been sporadic and based on comparatively few collections. Recent more extensive field work, first by the Marine Biological Survey of the University of Cape Town, and subsequently by Dr G. F. Papenfuss and the writer, have revealed many little-known or unnamed seaweeds; some of these have already been described (Kylin, 1938; Levring, 1938) but undoubtedly many, particularly among the smaller forms, still remain unnamed. Of the latter, the present paper deals with four only, all of which serve as hosts for parasitic Florideae collected during the past few years.

Study of these parasites showed that they are confined to specific hosts, most often, but not invariably, closely allied to the invading parasite; usually any one parasite occurs on one host only, occasionally on two nearly allied species and only rarely on a number of different species. It is obviously important to identify the host-alga, and in the effort to do so it was found that four at least of the hosts were as yet unnamed. These four, all as it happens members of the Rhodomelaceae, are dealt with here.

The classification followed is that given by De Toni (1903), which is itself based on the scheme given in Falkenberg's Monograph of the Rhodomelaceae (1901). The numbers quoted refer to specimens in the writer's herbarium, except where prefaced by the initials G.F.P. which refer to specimens in Dr Papenfuss's collection. In most cases the specimens quoted are representative of different localities and are not necessarily exhaustive.

Subfamily 3. POLYSIPHONIEAE

Rhodomelopsis Gen. nov.

Rhodomelopsis gen. nov. Frons erecta, carnoso-cartilaginea, teres, radialiter ramosa; axis polysiphonius, cellulis pericentralibus ?4 vel 7 (?6–8), cellulis centralibus aeque longis, ab apice usque ad basim cortice crassiusculo celluloso obvolutus, ramulis fertilibus exceptis. Crescentia terminalis monopodica, cellula apicali transverse septata: trichoblastae nullae, ramulis brevibus procarpia ferentibus exceptis, tum comae apicales si primo inveniuntur breves et mox evanescunt. Color frondis viventis plerumque fuscus vel obscure brunneus, expositione vel exsiccatione nigrescit.

Tetrasporangia in stichidiis omnino polysiphonis, ecorticatis vel solum partim corticatis, demum torulosis: tetrasporangia magna in segmentis singula, plerumque in una linea disposita.

Ramusculi antheridiales e segmentis cellularum apicalium ramorum parvorum et lateralium serie perpetua surgentes, non in trichoblastis.

Procarpium fert trichoblasta brevissima, ubi comae apicales si primo inveniuntur mox evanescunt. Cystocarpium globosum vel subglobosum, carpostomio vix protracto apertum.

Rhodomelopsis africana sp.nov. Plantae fruticosae robustae, ramis basica portione transversis, rhizomiformibus; saepe socialiter crescentes, crassam tegetem in planis saxi spatiis facientes, ibi fere 10 cm. altitudine, sed in lacunis profondioribus minus compactae et ad 20 cm. altitudine: natura carnosiores cum aridae sunt cartilaginosiores: colore plerumque fusco, aliquando subnigro: saxo solutae aut arefactae nigrescunt:

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[1] Part of this work was done while holding a Senior Bursary granted by the Council for Scientific and Industrial Research of South Africa for work on algae, both fresh-water and marine, in the United States of America and Australasia.

chromoplastae numerosae, parietales, grandiores, varia forma et magnitudine. Cellulae pericentrales 7, dense paene ad apicem corticatae. Trichoblastae perraro formatae, non etiam in plantis sexualibus conspicuae ubi breves nec nisi organa feminea ferentes inveniuntur. Ramos facit apex radialiter: organa generandi omnia in cristis ad extremitatem ramorum.

Planta tetrasporica tetrasporangia in stichidiis paene falcatis demum torulosis, fastigiatis, parte basica robustis non constrictis: singula segmentis tetrasporangia, ipsa magna, aliquantum regulariter in una linea sequentia; trichoblastae nullae.

Planta mas tetrasporicae aspectu persimilis, ramis qui antheridiales ramusculos ferunt in eodem situ et numero atque stichidiis formatis: ad apices multi ramuli feruntur qui ipsi multos ramusculos antheridiales ferunt, spiraliter ordinatos: maturi crassiores et falcati sunt, omnino spermatangiis obducti.

Planta feminea procarpia multa ad apices in trichoblastis brevissimis, comae apicales breves mox evanescunt. Cystocarpium ramo brevi laterali sessile, crassum et robustum, paene globosum, rostro paullum eminente cuius ad apicem est ostiolum.

Text-fig. 1; Pl. **5**, figs. A–F; Pl. **6**, figs. A–C.

Rhodomelopsis n.gen. Frond erect, fleshy-cartilaginous, terete, radially branched; axis polysiphonous, pericentral cells ?4 or 7 (?6–8), equal in length to the central cells; covered from apex to base with a fairly thick cellular cortex, fertile branches excepted. Apical growth monopodial, apical cell transversely septate: no trichoblasts except on the short branches bearing the procarps, then apical hairs, if at first present, short and soon shed. Colour of living frond yellowish brown to dark brown, blackening on exposure or on drying.

Tetrasporangia in stichidia, polysiphonous throughout, ecorticate or only partially corticate, eventually becoming torulose: tetrasporangia large, one per segment, usually arranged in a single row.

Antheridial branchlets arising in sequence from successive segments of the apical cells of small lateral branches, not on trichoblasts.

Procarp borne on a very short trichoblast, apical hairs if at first present soon shed. Cystocarp globose to subglobose with scarcely protruding carpostomium.

Rhodomelopsis africana n.sp. Robust bushy plants with basal system of horizontal rhizome-like branches; often growing socially to form a thick mat on flat rock ledges, then about 10 cm. in height, or if in deeper pools less compact and reaching as much as 20 cm. in height; consistency somewhat fleshy, tending to become cartilaginous on drying; colour usually yellowish brown, sometimes dark, blackening in drift or on drying; chromoplasts numerous, parietal, rather large, varying in size and shape. Pericentral cells 7, densely corticated to very close behind the apex. Trichoblasts very rarely formed, inconspicuous even in the sexual plants where they are short and formed only in connexion with the female organs. Branching of apex radial; all reproductive organs borne in clusters at the tips of branches.

Tetrasporic plant with tetrasporangia in somewhat falcate stichidia, eventually torulose, fastigiate, base robust not constricted; tetrasporangia one per segment, large, arranged more or less regularly in a single line; no trichoblasts.

Male plant very similar in appearance to the tetrasporic, the branches bearing the antheridial clusters being formed in similar position and number to the stichidia; at the apices many small branches are formed each of which gives rise to a number of antheridial branchlets arranged spirally; when mature comparatively broad, falcate, completely covered with spermatangia.

Female plant with many procarps at the apices borne on very short trichoblasts, apical hairs short and soon shed. Cystocarp sessile on a short lateral branch, large and massive, nearly spherical with slightly protruding beak at the apex of which the ostiole lies.

Occurrence. Characteristically found on rather soft rock, usually Dune Rock, often with a light covering of sand, either in low-tide pools or gullies just awash at low water, or on terraces or ledges covered with shallow pools or even exposed at low tide.

Geographical distribution. Widespread on the east coast from Arniston to Port St Johns, possibly extending to Natal. Locally sometimes very abundant, particularly at The Three Sisters (Riet River) east of the Kowie. Not uncommon in drift, then the taller and less compact form suggesting growth in the sublittoral zone; often with many epiphytes such as *Polyzonia elegans*, *Hypnea musciformis*, *Acrosorium* spp.

Recorded from: Arniston, deep intertidal pools in Dune-Rock terraces (1273 Type); Buffalo Bay (7709); Cannon Rocks, Richmond (7959, 8211); Bushman's River (6032, 6837); Kariega (5099); the Ship Rock, Kasouga (8162); Kowie (G.F.P. 1132), beyond Salt Vlei (4144, 6154); Kleinemonde (6366, 7420, 8400); Riet River, very abundant between the first and second of the Three Sisters (6398, 6949, 6951, 7481, 7556, etc.); Fish Point (8111); Waterloo Bay (8065); Hamburg (7384); Cove Rock near East London (7301, 8507, 8654, 9152); Hagahaga (3592); Morgan Bay (7104); Port Edward (10, 110).

TYPE LOCALITY. Arniston.

OBSERVATIONS. *R. africana* is a very distinctive little plant, characterized by its bushy habit, with basal system of rhizome-like axes, radial organization of the growing apex (Pl. **5**B)—the apparent dorsi-ventrality of the prostate shoots and of the fertile regions is purely secondary—the complete absence of hyaline hairs and trichoblasts except on the young procarp-bearing branches, the olive-brown colour readily blackening on exposure, drying, etc., and by the production of numerous reproductive organs in clusters at the tops of branches which are often longer than the vegetative axes (Pl. **5**A). This is specially marked in the tetrasporic and male plants which are much alike in appearance; in the former, however, the stichidia may persist after the spores are shed, whereas the antheridial branchlets drop off very early (Pl. **5**F; Pl. **6**A). The polysiphonous stichidia are at first completely ecorticate; later cortical cells may be cut off here and there and this condition may persist (Pl. **5**E, F), but sometimes a tetraspore-bearing branch may continue growth, giving rise to a cluster of secondary stichidia while it itself becomes fully corticated (cf. branch on right in Pl. **5**E). Thus, whereas in general the stichidia are well-defined, specialized branches, there may yet occur unmodified tetraspore-bearing branches similar to the type of sporiferous branches characteristic of the genera *Alsidium* and *Lophurella*. The tetrasporangia usually arise from a pericentral cell adjacent to the adaxial concave side of the young falcate stichidium and, since they are formed from corresponding cells of successive segments, they form a linear series, occasionally interrupted, and are not arranged spirally (Pl. **5**E). As development proceeds, however, the spores enlarge greatly and mutual pressure pushes them out of line, now to one side now to the other, and the protruding tetrasporangia, each with its two long cover cells, cause the stichidium to become torulose (Pl. **5**F).

In the male plant the complete absence of hair-bearing trichoblasts is characteristic, the antheridial branchlets arising directly from successive segments of the apical cell instead of laterally on a trichoblast; the whole branchlet, except for the two basal cells, eventually gives rise to spermatangia; the apical cell most often finally aborts without forming spermatangia. As in the tetrasporic plant, apical cells of the growing axes are naked, and this applies also to the female plant, except in the case of the small branchlets which actually bear the procarps; even there the trichoblasts are small and inconspicuous and the apical hairs short and fugitive. The arrangement of these fertile branchlets is particularly striking—they are formed in groups, each group being protected by the long sterile first-formed branches (Pl. **6**B), on the inner sides of which numerous small branchlets arise, and it is the apical cells of the latter which alone bear trichoblasts. The number of procarps in each cluster is large and only some of them develop into fully formed cystocarps; many begin to develop but abort before reaching maturity (Pl. **6**C). As the short hyaline hairs on the young trichoblasts are soon shed and are never conspicuous, even the female plant appears destitute of trichoblasts unless very young fertile apices are present. The cystocarps are large and so very nearly spherical that it is difficult to distinguish the very slightly protruding beak.

Rhodomelopsis undoubtedly stands very close to the genera *Alsidium* Agardh and *Lophurella* Schmitz. Like both these genera it is polysiphonous throughout with undivided pericentral cells, covered in all the vegetative parts from close behind the apex (eight to ten segments) with a cellular cortex of two or more series of cells (Pl. 5D); as in *Alsidium* the central axis is visible through the cortex, at least in the younger parts (Pl. 5B), branching is radial, and there are no trichoblasts and hyaline hairs on any of the vegetative axes (Pl. 5C). The sporangia are one per segment, but whereas in *Alsidium* and *Lophurella* the arrangement is spiral, in *Rhodomelopsis* it is linear; further, in the latter the sporangiferous branches are much modified and when young are ecorticate or only partially corticate, whereas in the two former they are scarcely modified but are similar in construction to and often continuous with the ordinary vegetative branches.

Examination of specimens of *Alsidium* in the Setchell collection in the University of California, at Uppsala, at Kew and at the British Museum of Natural History shows that, while there is certainly considerable resemblance in habit and size as well as in structure between the South African plant and *A. corallinum* Kützing (cf. in particular one specimen from Trieste in the herbarium at Uppsala labelled 'Herbar Hauck' and marked on the sheet 'Herb. J. E. Areschoug', and one or two plants, also from Trieste, in the British Museum), there is a most marked difference in colour; there is never any sign of the blackening so characteristic of our plant and the description given by Agardh (1863, p. 838; see also De Toni, loc. cit., p. 859) of the colour in *Alsidium* as 'when fresh, red-purple, easily fading when dried or exposed' is very different from the drab olive brown or dusky yellowish brown of *Rhodomelopsis*.

The colour and the tendency to blacken suggest affinity with *Lophurella*, but in that genus not only are there always four pericentral cells (regarded as a generic character by Schmitz), but all save one species, *L. patula* (Hook. f. et Harv.) (=*Rhodomela patula*) somewhat doubtfully included here by De Toni (loc. cit., p. 859), are characterized by good development of trichoblasts and apical hairs. Of *L. patula*, however Kylin (in Kylin & Skottsberg, 1919, p. 53) writes: 'A good species which differs from *L. Hookeriana* in the radial branching, not unilateral as in the latter species. From *L. comosa* (Hook. f. et Harv.) Falkenb., *L. patula* is distinguished by the absence of trichoblasts; in *L. comosa* numerous trichoblasts, usually shed late, are present. In *L. patula* I have searched for them in vain even in the young still growing apices.' In his later work Kylin regarded the presence or absence of trichoblasts as of prime diagnostic significance, and from his description it seems probable that *Rhodomela patula* Hook. f. et Harv. should not be included in the genus *Lophurella*, despite the number of pericentral cells. On the other hand, apart from the difference in number of pericentral cells, not necessarily constant within a genus, it has obviously several characters suggesting a closer affinity with the South African plant and it seems possible that it should therefore be associated with it in the new genus *Rhodomelopsis*. Unfortunately the material representative of the genus *Lophurella* at present available for study does not include *L. patula* and, pending a careful study of the actual plant, it is only possible to suggest tentatively that the transfer may be justified.

Although the South African plant is not closely allied to the genus *Rhodomela* there is a superficial resemblance, hence the choice of the generic name *Rhodomelopsis*.

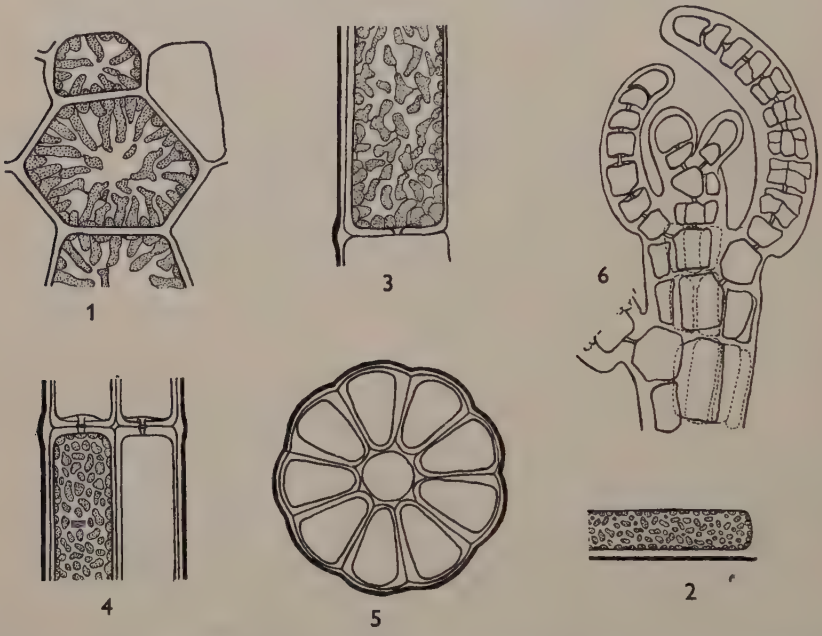
Subfamily 9. HERPOSIPHONIEAE

Placophora J. Agardh

Placophora eckloniae sp.nov. Thallus planus, multum lobatus, puniceo colore, spatiis *Eckloniae maximae* stipitis grandibus obductus, cellulis pericentralibus 5, tribus dorsalibus duplo latioribus quam ventralibus duobus, cellula centrali etiam angustiore. Emittunt cellulae pericentrales ventrales organa tenacia permulta: e cellulis dorsalibus surgunt rami fertiles, cristas in superficie thalli prope margines lobarum densissimas formantes. Habent hi rami cellulas pericentrales 5–8, saepenumero 6–7; nullas trichoblastas nisi ramusculos breves procarpia ferentes.

Thallus tetrasporicus axes fertiles longiores ad 1 cm., simplices primo aut interdum ramosos, tum ramulos laterales breves ferentes, axes omnes et ramulos per totam longitudinem fertiles, paucis segmentis basicis (5–10) exceptis: singula segmentis tetrasporangia recta linea sese sequentia.

Thallus mas axes fertiles breviores quam tetrasporicus aut femineus habet: trichoblastas nullas, ramusculos antheridiales a cellula apicali successione radiali sese formantes, cum maturi sunt elongatos, curvatos, pediculo unicellulari, apice attenuato.



Text-figs. 1–4. Cells showing form of the chromoplasts. Text-fig. 1. *Rhodomelopsis africana*. Text-fig. 2. *Placophora ecklonaiae*. Text-fig. 3. *Streblocladia tenuissima*. Text-fig. 4. *Falkenbergiella caespitosa*. Text-fig. 5. *Streblocladia tenuissima* transverse section near base of free axis. Text-fig. 6. *Placophora ecklonaiae* diagram of apex of fertile male axis showing development of antheridial branchlets. All × 500.

Thallus femineus axes fertiles nunquam breviores, interdum longiores quam tetrasporicus habet, ramosos nonnunquam, procarpia compluria singulos ferentes et saepenumero ramulos laterales. Cystocarpium paene fusiforme est sed rotundius, brevi pediculo, apice eminente.

Text-figs. 2 and 6, Pl. 7, figs. A–H.

Placophora eckloniae n.sp. Thallus flat, extensively lobed, red in colour, covering considerable areas of the stipe of *Ecklonia maxima*; pericentral cells 5, the 3 dorsal twice as wide as the 2 ventral, the central cell narrower. From the ventral cells grow short attachment organs in great numbers, from the dorsal cells arise fertile branches forming very dense tufts on the surface of the thallus near the margins of the lobes. These branches have 5–8 pericentral cells, often 6–7: no trichoblasts except on the short branchlets bearing the procarps.

Tetrasporic thallus with comparatively long fertile axes, up to 1 cm., at first simple or occasionally branched, later bearing short lateral branchlets, all axes and branches fertile throughout their length except for a few (5–10) basal segments: tetrasporangia one per segment, in rectilinear sequence.

Male thallus with fertile axes shorter than the tetrasporic or female: no trichoblasts, antheridial branchlets formed in radial succession from the apical cell, when mature elongated, curved, with unicellular stalk and attenuated apex.

Female thallus with fertile axes as long as or longer than the tetrasporic, occasionally branched, each bearing several procarps and often lateral branchlets. Cystocarp almost fusiform but rounder with short stalk and protuberant apex.

OCCURRENCE. On the stipe of *E. maxima*, occasional, but when present covering large areas of the upper part of the stipe; when fertile forming over the surface a thick shaggy felt as much as 1 cm. or more in depth.

GEOGRAPHICAL DISTRIBUTION. Probably to be expected wherever the *Ecklonia* occurs. Hitherto found only in drift at Muizenberg (7825 Type, 7828, 9216), Strandfontein (6673), Hout Bay (9203), Maclear's Beach (9235) and Sea View near Port Elizabeth (8420); and attached at Blaauwberg Strand (8183) and at Strandfontein (9260).

TYPE LOCALITY. Muizenberg.

OBSERVATIONS. *Placophora eckloniae* is noteworthy for the thick red felt formed by the fertile axes, often covering large areas of the stipe on which it is growing; the basal part of the thallus is very similar in construction and mode of growth to that of *P. binderi*, but probably owing to the difference in habitat may be very much more extensive, while the fertile axes are considerably longer than in the latter species (Pl. 7A). While it is often difficult to determine the limits of an individual thallus owing partly to the extensive lobing, partly to the fact that it is often obscured by the felt of fertile branches and by one thallus overlapping another, and also by the growth of other algae which evidently find it an excellent substratum on which to obtain a foothold, it is sometimes possible to determine the extent of a single plant; some recently collected at Maclear's Beach were free both of fertile branches and epiphytes and several thalli each covered as much as a square inch of the stipe on which they were growing, possibly even more. The attachment to the substratum is extraordinarily close; a transverse section shows the expanded disk-like tips of the attachment organs forming an almost continuous layer over the surface of the stipe, from which the thallus is separated by the short parallel props formed by the tubular upper parts of the holdfasts. It is thus extremely difficult and usually impossible to detach complete plants from the host. The long, several-celled attachment filaments characteristic of *Placophora binderi* when growing on *Codium* are absent in *P. eckloniae* or occur only occasionally in a modified form, much shorter in length, when another *Placophora* thallus serves as substratum.

Our plant differs further from *P. binderi* not only in the greater length of the erect fertile axes but also in their far greater number, their frequent branching and their position on the dorsal surface of the frond, parallel to the margin, which continues growth, instead of in rather small tufts at the base of notches between lobes as is more usual in *P. binderi* (Pl. 7B). As marginal growth progresses, new branches continue to arise from the dorsal cells of the thallus behind the margin until the thallus may be more or less covered, the earlier formed branches continuing to grow in length. Further the colour is a rich red considerably lighter and brighter than that of the latter species, which often tends to be dark reddish brown, darkening on exposure.

In the asexual plant the continued growth of the erect fertile branches, accompanied by the formation of short stichidia-like laterals, is very characteristic (Pl. 7C, D). As in *Rhodomelopsis* the antheridial branchlets arise directly from initial cells cut off in radial sequence from segments of the apical cell (Text-fig. 6). Each initial cell gives rise to a short branch of from 12 to 14 cells; the basal cell forms the supporting cell within the tissue of the parent branch, the second cell forms the short stalk and the three or four apical cells remain undivided. The intervening cells cut off pericentral cells and eventually produce spermatangia. The mature antheridial cluster is elongated, curved and at the end has a short projecting monosiphonous row of three or four cells, i.e. here the antheridial branchlet may be regarded as an unbranched trichoblast with a very short apical 'hair'. The basal supporting cell enlarges, pushing the short pericentral cell below it downwards and the one above it upwards out of line with the other cells of the two segments. As growth of the fertile axis proceeds, the older antheridial clusters drop off, leaving the basal cell as a small projecting shelf which gives the male fertile branches a most characteristic appearance (Pl. **7** E, F). In the female plant the procarp is formed as usual on the second segment of a trichoblast which continues as a delicate branch of a few hyaline cells; these in turn give rise on the adaxial side to two or three similar branches or hairs. At an early stage of development of the cystocarp the whole of this upper part of the trichoblast drops off leaving no trace. The basal segment forms a massive stalk at right angles to the erect axis and on this stalk the cystocarp grows erect (Pl. **7** G, H).

The genus *Placophora* is regarded as monotypic by De Toni (loc. cit., p. 1044); *P. eckloniae* is apparently confined to the stipe of *Ecklonia*, whereas *P. binderi* as at present accepted occurs on a variety of hosts in addition to the various species of *Codium* on which it is commonly found, for example, *Gelidium cartilagineum* and *G. amansii*, *Amphiroa bowerbankii* and *A. ephedra*, *Zonaria subarticulata*, and on the horny skeleton of *Pyura*. Some characters, in particular the nature of the attachment organs, appear to vary according to the nature of the host, and a closer study of the different forms may possibly show that the specific '*Binderi*' actually includes a complex of species.

Placophora eckloniae often serves as substratum for sporelings of *Tayloriella virgata* (Ag.) Papenfuss and is often, though not invariably, found in association with that plant; when growing on *Placophora*, *Tayloriella* is often precocious, becoming fertile while still barely a centimetre or two high, and in this state it is sometimes easy to confuse reproductive organs of the two plants, which, despite their very different habit, seem to be somewhat closely allied. This is also suggested by the fact that *Placophora eckloniae* may serve as an alternative host to *Stomatocarpus parasiticas*, hitherto known only as a parasite of *Tayloriella virgata*.

Streblocladia Schmitz

Streblocladia tenuissima sp.nov. Thallus tenuissimus, totus ecorticatus, parte inferiore algis maioribus obducta, organo tenaci tubulato, unicellulari, expanso ad finem in disculum ramosum: ramos longis intervallis inferiore parte supra brevioribus formans, per totam stirpem pseudodichotomus, ramis lateralibus haud minus quam axe ipso vegetis: ramis ultimis perquam exilibus: roseo colore, chromoplastis variis, plerumque elongatis, nonnunquam ramosis aut brevibus et rotundatis: cellulae pericentrales 7–10, plerumque 9, omnino ecorticatae: segmentis fere 1½ plo diametro longioribus.

Thallus tetrasporicus ramos fertiles vix ramis liberis dissimiles, in cristis ad extremitates eorum habet: singula segmentis sporangia recta linea sese sequentia: comas apicales plerumque nullas sed aliquando bene formatas.

Thallus mas similis aspectu tetrasporico, identidem ramos ad apices axium emittit, cristas ramulorum spissas formantes quorum ad extremitates ramusculi antheridiales multi grandiores paene recti formantur.

Thallus femineus comas apicales plerumque bene formatas habet: procarpia multa in regione ramosa distali saepe sed non semper latere adaxiali rami formata. Cystocarpium paene globosum, tam latum quam longum aut etiam latius, apice non eminente, carposporis parvis permultis.

Text-figs. **3**, **5**; Pl. **6**, fig. D; Pl. **8**, figs. A–F.

Streblocladia tenuissima n.sp. A very slender plant, lower portion spreading over and attached to larger algae; attachment organ tubular, unicellular expanded at the end into a small branched disk: branching in the lower part at long intervals, closer above, throughout pseudodichotomous, the lateral branches growing almost as strongly as the main axis: ultimate branches exceedingly fine: colour rosy red, chromoplasts various, mostly elongate, occasionally branched, or short and rounded: pericentral cells 7–10, most often 9, ecorticate throughout, length of segment approximately 1½ times the diameter.

Tetrasporic thallus with fertile branches in tufts at the tips of the free axes, scarcely modified: sporangia one per segment, in rectilinear sequence. Apical hairs normally absent but occasionally present and well developed.

Male thallus very similar in appearance to the tetrasporic, repeated branching towards the apices of the free axes resulting in the formation of close tufts of small branches at the tips of which numerous rather large, nearly straight antheridial branchlets are borne.

Female thallus with apical hairs usually well developed, procarps numerous in the much branched distal region, often developed on the adaxial side of the branch but not invariably so. Cystocarp globular, as broad as long or even broader, apex not protuberant, carpospores small, very numerous.

OCCURRENCE. Very characteristic in habit, epiphytic on other Red Algae such as *Rhodomelopsis africana*, species of *Tayloriella* and *Pterosiphonia* growing on sand-washed rock in gullies or low-tide pools. Host plants sometimes completely buried at low water, the fine red hair-like branches of the epiphyte alone projecting, often lying on the white sand as a wave recedes and more conspicuous under such conditions than when actually in water. In deeper pools waving in the water one or two inches above the top of the host plant.

GEOGRAPHICAL DISTRIBUTION. Apparently confined to the east coast and as yet collected only in three localities but easily overlooked and probably more widespread than would appear. Found at Cove Rock, near East London (in sandy gully separating the Rock from the mainland), abundant (7309, 8489 Type, 9145); Hamburg, occasional (8610); Riet River in open rock-floored bay between the second and third of the 'Three Sisters'.

TYPE LOCALITY. Cove Rock.

OBSERVATIONS. The extreme slenderness of this little plant (Pl. **6**D) makes it very easily overlooked, although the bright red colour contrasting with the dark fuscous brown of the larger algae on which it usually grows makes it less inconspicuous than might be expected from its size and diffuse habit. The pseudodichotomous branching of the whole plant, the repeated branching at the apices of fertile plants with the resultant formation of 'brushes' of fertile branchlets (Pl. **6**D; Pl. **8**A–C, E) and the spiral twisting of the axes particularly in sterile plants are very characteristic. The spiral appearance of the pericentral cells of a segment may also show to less degree in fertile regions (Pl. **8**B, C). The small globular cystocarps are unusually broad in proportion to their size; in position most often adaxial, they may, however, be formed on the abaxial side of a branch as well; size and varying position are shown in the series of photographs (Pl. **8**D–F).

Streblocladia tenuissima acts as host to a small species of *Microcolax* which parasitizes the upper branches, on which numerous diatoms, particularly a species of *Licmophora*, also find a home. The parasite has been found only at Cove Rock and even there it is rare.

Falkenbergiella Kylin

Falkenbergiella caespitosa sp.nov. (Lat. caespes, a turf, in reference to its characteristic habit.) Planta parva caespitosa, cellulis pericentralibus 4: e portione inferiore axibus dense implicatis serpentibus rhizomiformibus formata surgunt rami erecti permulti, plerumque 1 cm. aut minus altitudine, tandem ad 1½–2 cm., rare altiores: apex crescens serpentium axium paullum deprimitur vel interdum rectus: ramificatio endogena, ramuli fertiles erecti dorsuales, rami serpentes aut dorsuales aut laterales oriuntur, rami primo ad apicem versus inclinati vel paullum curvati: rami erecti primo simplices sunt postea perquam ramosi: organa tenacia unicellularia tubularia disco peltato terminata: adsunt trichoblastae sed solum in ramis fertilibus et tetrasporicis et femineis saepe evanescunt praecipue cum alga inter alias algas crescit, in unda aperta saepe persistunt, comas hyalinas bene formatas ferentes: chromoplasta multa exigua disciformia, color plantae viventis subfuscus aut flavus, exsiccatione nigrescit.

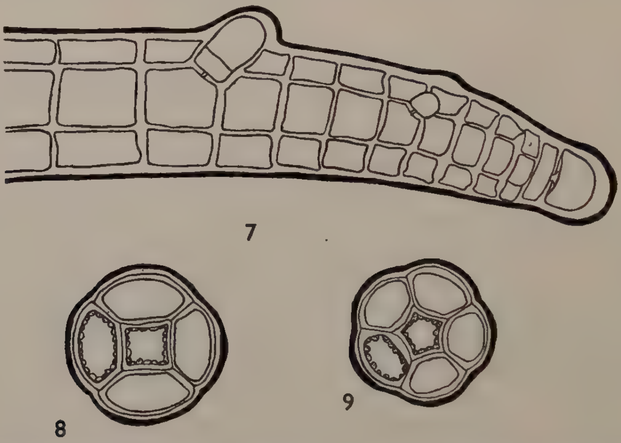
Thallus tetrasporicus tetrasporangia in ramis falcatis plerumque habet, cristas summis in axibus spissas formantibus: singula segmentis sporangia recta linea sese sequentia, aliquando interrupta.

Thallus mas axes erectos habet identidem ramosos, trichoblastas nullas: ramusculi antheridiales multi ad apices, e segmentis cellulae apicalis serie perpetua surgentes, elongati sed latiores, paullum curvati.

Thallus femineus axes erectos aut simplices aut raro aut identidem ramosos habet: procarpia in ramulis brevibus lateralibus compluria in ramis singulis non in uno tantum latere: trichoblastae comas hyalinas ferentes brevi decidentes. Cystocarpium oviforme, basi lata et apice angustiore et rotundato.

Text-figs. 4, 7–9; Pl. **9**, figs. A, H.

Falkenbergiella caespitosa n.sp. A small caespitose plant with four pericentral cells: from the lower portion composed of densely interwoven creeping rhizome-like axes arise numerous erect branches usually 1 cm. or less in height, ultimately reaching as much as 1½ or 2 cm., rarely more; growing apex of prostrate axis slightly depressed or sometimes straight; branching endogenous, erect branches dorsal, prostrate branches either dorsal or lateral in origin, branches at first inclined or slightly curved towards the apex; erect branches at first simple, later very much branched; attachment organ unicellular ending in a peltate disk; trichoblasts present but only on fertile branches both tetrasporic and female, often evanescent particularly when growing among other algae, in open water often persistent bearing well-developed hyaline hairs; chromoplasts numerous small disciform, colour of living plant brownish or yellowish brown blackening on drying.



Text-figs. 7–9. *Falkenbergiella caespitosa*. Text-fig. 7. Apex of prostrate axis showing initial cells of two erect branches. × 750 approx. Text-figs. 8, 9. Transverse sections of erect tetrasporic axes. Text-fig. 8 near the base, Text-fig. 9 through a sterile segment in the fertile region. × 500.

Tetrasporic thallus with tetrasporangia usually in falcate branches formed in tufts at the tips of the erect axes: sporangia one per segment in rectilinear sequence, sometimes interrupted.

Male thallus with repeatedly branched erect axes, no trichoblasts: antheridial branchlets numerous arising at the apices from successive segments of the apical cell, elongated but comparatively broad, slightly curved.

Female thallus with erect axes either simple, sparingly or much branched: procarps on short lateral branchlets several per branch, not confined to one side: trichoblasts bearing hyaline hairs, soon deciduous. Cystocarp ovate with broad base and narrower rounded apex.

Occurrence. On rock between tide marks or just below low tide, most often at the margins of reefs, on ledges or isolated boulders just awash at low water. Typically covering the surface of the rock like a dense mossy turf, often in pure stands, or mixed with other algae such as small species of *Gelidium*, *Centroceras clavulatum*, etc. Slightly higher up the shore it may be found growing among larger algae which protect it during periods of exposure between tides—at Muizenberg, the type locality, it was first found on the rocks just below the steps leading from the station to the beach growing among comparatively large plants of *Polysiphonia incompta* and a species of *Ophidocladus*, while lower down on the shore it covers ledges with a mossy growth, in places almost unmixed with other algae.

GEOGRAPHICAL DISTRIBUTION. Widespread on the coasts of South Africa: range as at present known from Blaauwberg on the west coast to Port St Johns on the east, probably even farther in both directions. Collected from the following localities. *Western Province*: Blaauwberg (8179); Muizenberg (7831, 8569 Type); Strandfontein (9256); Jeffrey's Bay (8308). *Eastern Province*: Cannon Rocks, Richmond (7993); Kasouga, the Ship Rock (8244); Kowie, beyond Salt Vlei (8460); Fish Point (8029); Waterloo Bay (8059); Cape Morgan (9293); Port St Johns (8829).

TYPE LOCALITY. Muizenberg.

OBSERVATIONS. *Falkenbergiella caespitosa* is characterized by the extremely well-developed prostrate system, the rhizome-like creeping axes typically forming a densely interwoven mat from which the potentially fertile, erect branches arise. The interval between branches varies enormously, probably determined by conditions of growth and environment. The branch initial is cut off from the central cell several segments behind the apical cell and usually develops at once, but may remain dormant (Text-fig. 7). Occasionally branch initials are cut off in successive segments but more usually several segments, varying from one to eight or nine, but most often three or four, intervene between branches (Pl. **9** D). In general only one branch is formed per segment, but even to this rule there are exceptions and very occasionally two branches may arise from the same central cell, emerging on opposite sides of a dorsal pericentral cell.

The young branch is sometimes curved but more often is nearly straight and inclined towards the apex of the prostrate axis; as in the other species the basal segment of the branch is incomplete with only the two abaxial pericentral cells present. These make contact with the two adjacent pericentral cells of the segment in which the branch is formed. Succeeding segments have the normal number, four, of pericentral cells.

The young sterile plant (Pl. **9** A) shows a dense felt of short erect unbranched axes the apices of which, like those of all prostrate axes, are 'bald' owing to the complete absence of trichoblasts and apical hairs; soon, however, if the plant is tetrasporic or female the tips of the erect branches begin to produce trichoblasts (Pl. **9** F, G) and close examination reveals the presence of tetrasporangium- or procarp-initials (Pl. **9** G, H). At the same time the number of pericentral cells increases to five (compare Text-figs. 8, 9). At first the erect branches are simple, completely devoid of laterals, but once they have become fertile branching begins, and soon each may become a richly branched system with long hyaline hairs surrounding each apical cell. This is especially marked in the tetrasporic plant where copious branching usually results in dense tufts of rugose, more or less falcate, stichidia-like branches, each with a row of large tetrasporangia (nearly mature tetrad $74 \times 66\mu$); occasionally sterile zones with only four pericentral cells per segment may intervene between fertile regions (Pl. **9** B, E, G).

Similar branching is found in the male plant, which, however, is distinguished from the others by the absence of apical hairs. This difference shows strikingly in the photograph of a hermaphrodite plant where a male branch occurs on an otherwise female plant (Pl. **9** H). As in *Rhodomelopsis africana* and *Placophora eckloniae* the antheridial branchlets arise in radial sequence directly from segments of the apical cell. Here the branchlet consists of eight to ten cells of which, as in those two species, the basal cell remains within the tissue of the parent axis while the second cell elongates considerably to form the monosiphonous stalk; formation of pericentral cells begins near the middle of the branchlet on the abaxial side and extends in both directions; eventually all the remaining cells, including the apical cell itself, are covered with spermatangia so that here there is in general no trace of an apical hair. Very occasionally, however, even here one or two cells at the apex do not divide but remain as a rudimentary hair projecting beyond the spermatangial mass. The mature antheridial cluster is comparatively large—about 55μ wide by 390μ in length.

Falkenbergiella caespitosa agrees closely with Kylin's genus in general habit and structure: in the dorsiventral organization of the thallus with two kinds of axes, both endogenous in origin, with four undivided pericentral cells completely ecorticate; basal segment of each branch with only two pericentral cells, and the complete absence of trichoblasts in the sterile condition. From *F. capensis* Kylin it differs in: (1) its habitat, the latter species having as yet been recorded only as growing on the horny outer case of the Tunicate *Pyura stolonifera* ('Red Bait'); (2) probably connected with this, the form of the attachment organ which ends in a peltate disk with short marginal branches, whereas in *Falkenbergiella capensis* the widened tip continues as two or more rather long tubular branches; (3) its larger size, erect branches up to 1 cm. or more in length as compared with 3–5 mm. in *F. capensis*; (4) erect axes unbranched in the sterile condition; (5) apex of prostrate axis slightly depressed or straight, whereas in Kylin's species it is normally bent upwards and more or less inrolled; and (6) position and shape of the rather large cystocarp (up to 300μ wide by 330μ long, with large pear-shaped carpospores 31$\mu \times$98μ when nearly mature (Pl. **9**C, G). Kylin gives no description of the antheridial branchlet in his species nor is there any information on this point available for either of the Australasian species.

With regard to the two latter, *Lophosiphonia prostrata* (Harv.) Falkenberg and *L. macra* (Harv.) Falkenb. which Kylin transferred to his new genus *Falkenbergiella*, in both the apex is not inrolled but straight or occasionally even slightly depressed as in *F. caespitosa*. This character must therefore be regarded not as generic but as specific to *F. capensis*, and the generic diagnosis amended accordingly. Even in the latter species it is not an invariable feature as straight apices may occasionally occur. From the accounts given by Falkenberg and De Toni, *F. prostrata* appears to be a larger but lower plant, the figure '2–5 cm.' evidently referring to the length of the thallus, while the erect branches are described as 'extremely short'. Further, it is apparently always epiphytic on *Gymnosorus nigrescens*, and the relation of the pericentral cells to the substratum is said to be constant, two cells ventral against the surface of the *Gymnosorus* frond, two dorsal, with the erect branches emerging between the two latter cells; in no other species is the relation a constant one, in all twisting of the axis may change the orientation of the pericentral cells from time to time. When it is as in *Falkenbergiella prostrata* there is a single row of dorsal branches and two rows of attachment organs. Should, however, the orientation be such that there is a single dorsal and a single ventral pericentral cell, there would necessarily be two rows of dorsal branches and a single row of attachment organs. One or other arrangement is apparently dominant in any one species, but in all except *F. prostrata* there is considerable variation and both types of organization may occur in each species.

Turning finally to *F. macra* (Harv.) Kylin, it is found that it and *F. caespitosa* have many features in common. Apparently the original material on which Harvey founded his species was immature and still sterile since no mention of reproductive organs is made. Fortunately, material from Long Beach, Russell, Bay of Islands (Lindauer, Fasc. 4, no. 96), though in part young, includes good tetrasporic specimens, a study of which has made possible a more complete comparison with the latter species than would otherwise have been possible. In both, the habit is the same—a dense mat of interwoven creeping axes from which arise masses of erect potentially fertile short axes, in the sterile condition unbranched and completely devoid of trichoblasts, but in both, with the onset of fertility, in the tetrasporic plant at any rate, branching begins and trichoblasts are formed. The branching appears less copious and the formation of hair-bearing trichoblasts far less rich in *F. macra* but this may well be a function of age or external conditions and the general behaviour is the same in the two species. In the New Zealand plant there appears to be usually a single row of erect dorsal axes, while the prostrate axes usually arise laterally, but despite Harvey's description and Falkenberg's statement to the contrary, this is not invariable and dorsal axes may at times grow horizontally instead of vertically. The arrangement of the attachment organs in two rows is made very obvious by the fact that frequently two such organs are formed side by side on the same segment, growing out at an angle to one another—a feature not as yet noted in either of the South African species in both of which there are most often two rows of erect dorsal branches and a single row of attachment organs, the latter nearly always originating from the branch-bearing segment.

It is thus obvious that *F. caespitosa* is very close to *F. macra*; it differs from the latter however in a number of details, viz. (1) habitat, usually on sand-washed rock as compared with 'clean rock' (Lindauer) or a substratum of Cyanophyceae (Harvey); (2) colour, dull fuscous olive brown to yellowish brown, whereas the New Zealand plant is a rich reddish brown when dry, probably brighter when living; (3) rather larger size (10–15 mm. or more when well developed as compared with 7–10 mm. in *F. macra*); (4) apex most often depressed instead of straight; (5) most often two rows of dorsal branches and one row of attachment organs, whereas in *F. macra* the more usual arrangement is one row of dorsal branches and two rows of attachment organs, often two from a single segment; (6) segments rather longer in proportion to their breadth (*F. caespitosa*, prostrate axes: segment 66–94μ wide by 62–214μ long; erect axes: 58–81μ by 81–133μ. *F. macra*, prostrate axes: segment 62–120μ by 75–140μ; erect axes 51–58μ by 24–26μ); (7) more copious branching and richer development of trichoblasts with long hyaline hairs in both tetrasporic and female plants; and (8) wall of older prostrate branches colourless and hyaline, whereas in *F. macra* it tends to become yellowish brown and very thick. The differences are small but cumulative and therefore the South African plant is regarded as worthy of distinct specific rank.

Small as it is, *F. caespitosa* acts as host to a small parasitic red alga of a new type to which the generic name of *Aiolocolax* has been given and which has been found almost wherever the host plant occurs.

Discussion

The four members of the Rhodomelaceae described here have been brought together solely because all act as hosts to parasitic Florideae, hitherto undescribed or unrecorded, but curiously enough all have certain features in common, in particular the absence of trichoblasts in the sterile condition. In three of them this applies also to the male plant even when fertile, taking the term 'trichoblast' to indicate the characteristic apical branches bearing long hairs which protect the apex in, for instance, the members of the genus *Polysiphonia*. In these three the antheridial cluster, instead of being borne laterally on such a trichoblast, develops directly from a segment of the apical cell. In the more restricted sense, therefore, the antheridial branchlet may be regarded as representing a complete unbranched trichoblast, instead of a lateral branch of a trichoblast.

Two of the four algae are widespread: one, *Falkenbergiella caespitosa*, perhaps the commonest and most widely distributed of all South African seaweeds, yet apparently it has never been collected; it appears in none of the herbaria nor has there been found any description of a South African alga which might have applied to it. Reasons why it has been overlooked, however, are not hard to find since its small size, dull colour and to some extent the type of habitat it most frequents (rocks away from the main reefs) make it easily overlooked. It comes very close to the little-known New Zealand species *F. macra* which, however, is very different in colour and less inconspicuous than the South African plant.

It is more difficult to account for the neglect of *Rhodomelopsis africana* which is also widespread, but only on the south and east coasts where it is by no means rare, often present in abundance in intertidal pools and not uncommon in drift, particularly at Sharks Bay near the Kowie as well as at other favourite haunts of such keen collectors as Tyson, Flanagan and Becker. Yet it appears in none of their herbaria so far examined. It seems most improbable that it is a new-comer to these coasts and it is difficult to account for this attractive little plant being overlooked by these ardent collectors.

In the case of the two remaining plants, both are more restricted in occurrence: *Placophora eckloniae* is very specialized in its habitat and if noticed on the stipes of cast-up Sea Bamboos has probably been passed over as merely a rather large form of *P. binderi*, from which, however, it differs in many respects. Finally, *Streblocladia tenuissima* is apparently confined to a few stations on the east coast in a part where comparatively little collecting has as yet been done so that it may prove to be commoner than at present appears; it is extremely delicate, as the name implies, the ultimate branches of hair-like fineness, and it is only made apparent by the contrast of its bright red colour to the dark fuscous hue of the largar algae on which it normally grows.

One point which has been forced on one's notice in the course of this work is the need for a fuller re-investigation of many existing species, whether new or long established; many were originally made from a single collecting, often very incomplete, or from a few specimens not necessarily representative. As a result, the descriptions are often inadequate or not of general application. This was stressed by Dr G. F. Papenfuss at the Pacific Science Congress in 1949, primarily in connexion with Pacific marine algae, but is equally applicable to South African seaweeds. The state of affairs is well illustrated by a consideration of the three small algae included by Kylin in his genus *Falkenbergiella*, especially in the case of *F. macra*. Harvey founded his species, *Polysiphonia macra*, on material collected in New Zealand at Akaroa in the South Island and Hawkes Bay in the North, but evidently his material was so immature that no reproductive organs at all were present and no particulars of these appear in any of the existing descriptions; subsequent transfers, first by Falkenberg to the genus *Lophosiphonia* and more recently by Kylin to *Falkenbergiella* have been made entirely on vegetative characters. Hence an amplification of the original description, based on a careful study and re-examination of material, preferably living, from the type localities is urgently needed. The same applies, though in less degree, to *F. prostrata* from West Australia, while even in the type species, *F. capensis*, the description is incomplete, neither male plants nor mature cystocarps having been included, so that further study of this plant too is needed.

SUMMARY AND CONCLUSION

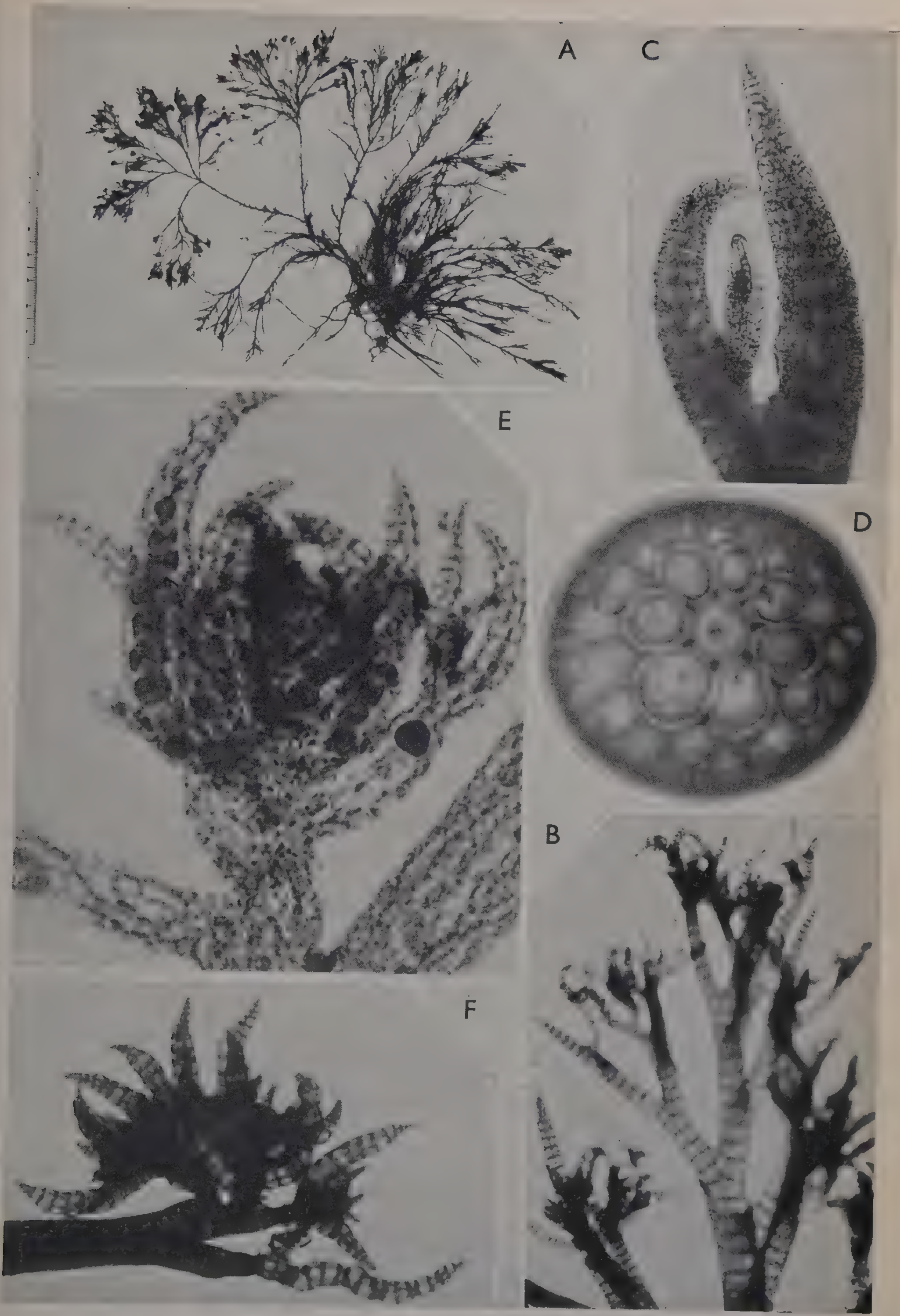
Four species of algae belonging to the Rhodomelaceae, very different from one another in habit, but all serving as hosts to parasitic Florideae, are described and observations on their occurrence and distribution, based on extensive field studies and collections, recorded.

For the first, widespread on the east coast, a new genus, *Rhodomelopsis*, allied to *Alsidium* and *Lophurella*, is created, with the single species *Rhodomelopsis africana*, but the suggestion is tentatively made that the plant *Lophurella patula* should probably be transferred to the new genus.

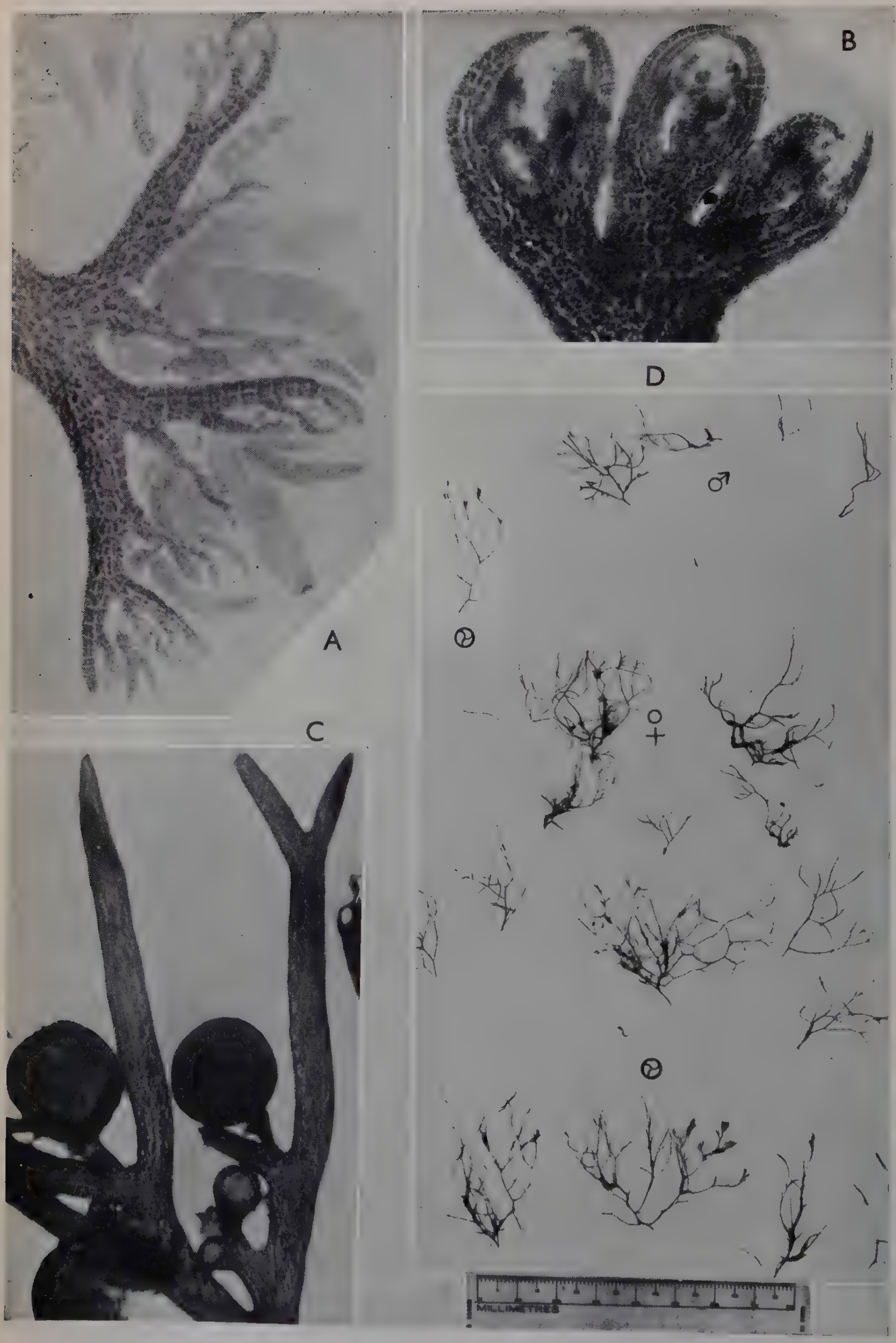
Of the remaining three species, *Placophora eckloniae* occurs in quantity on many stipes of *Ecklonia maxima* and is to be expected wherever that plant occurs, *Streblocladia tenuissima* appears to be restricted to a few localities on the east coast, while the last, *Falkenbergiella caespitosa*, is probably one of the commonest and most widespread of South African seaweeds.

The necessity for further study and amended descriptions of many existing species is urged, the genus *Falkenbergiella* and the three species included therein being quoted in illustration.

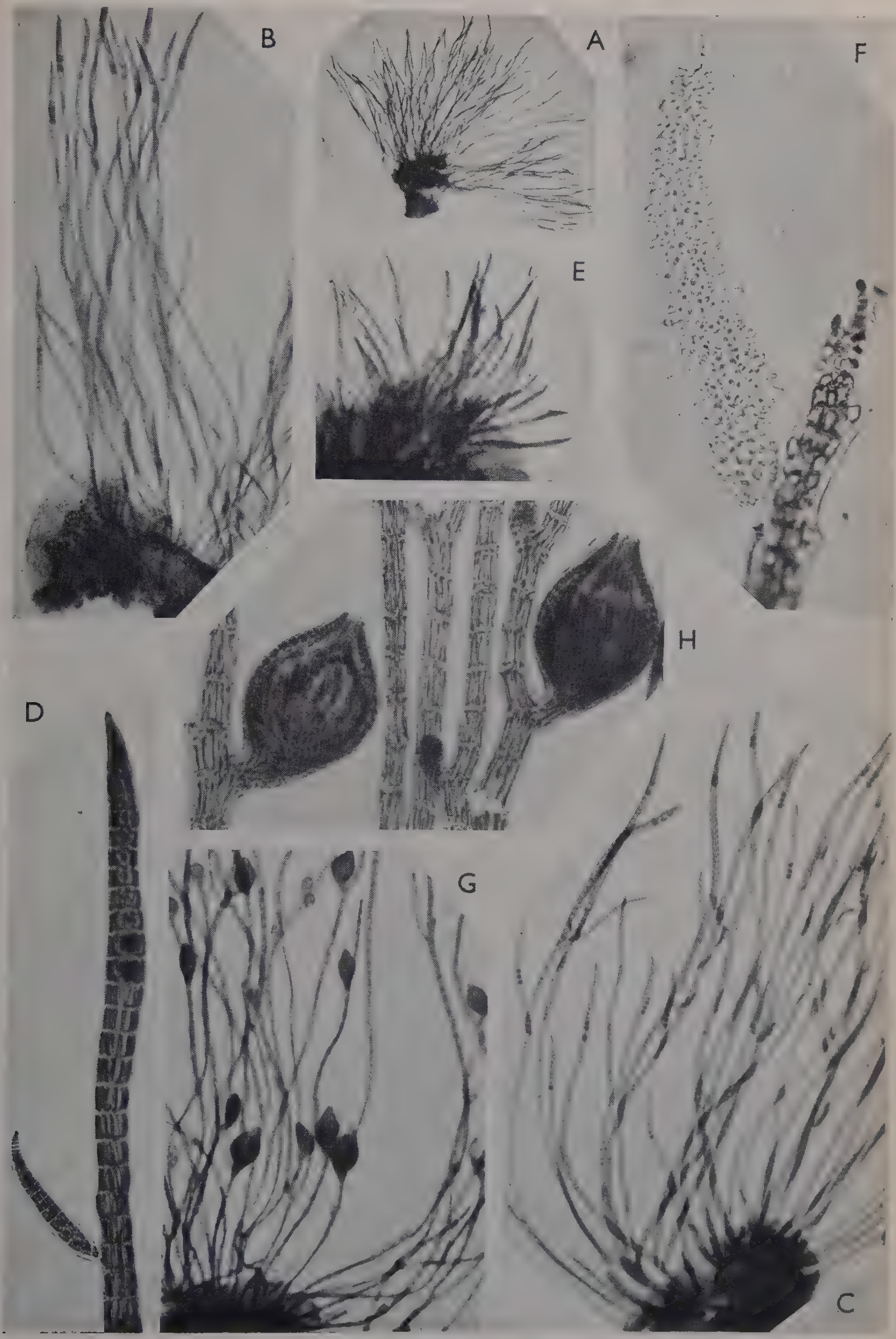
In conclusion it remains to express my grateful thanks to various helpers: to my brother, Prof. L. G. Pocock of Canterbury College, Christchurch, New Zealand, and to Mrs E. M. Wisbey for the Latin descriptions; to Mr Victor Lindauer for material of New Zealand algae including specimens of *Lophurella* and *Lophosiphonia* used in the course of this work; to Dr G. F. Papenfuss for much help and encouragement; and finally to Dr Lee Bonar of the University of California for the hospitality of the Botany Department of that university where a part of the work was done.



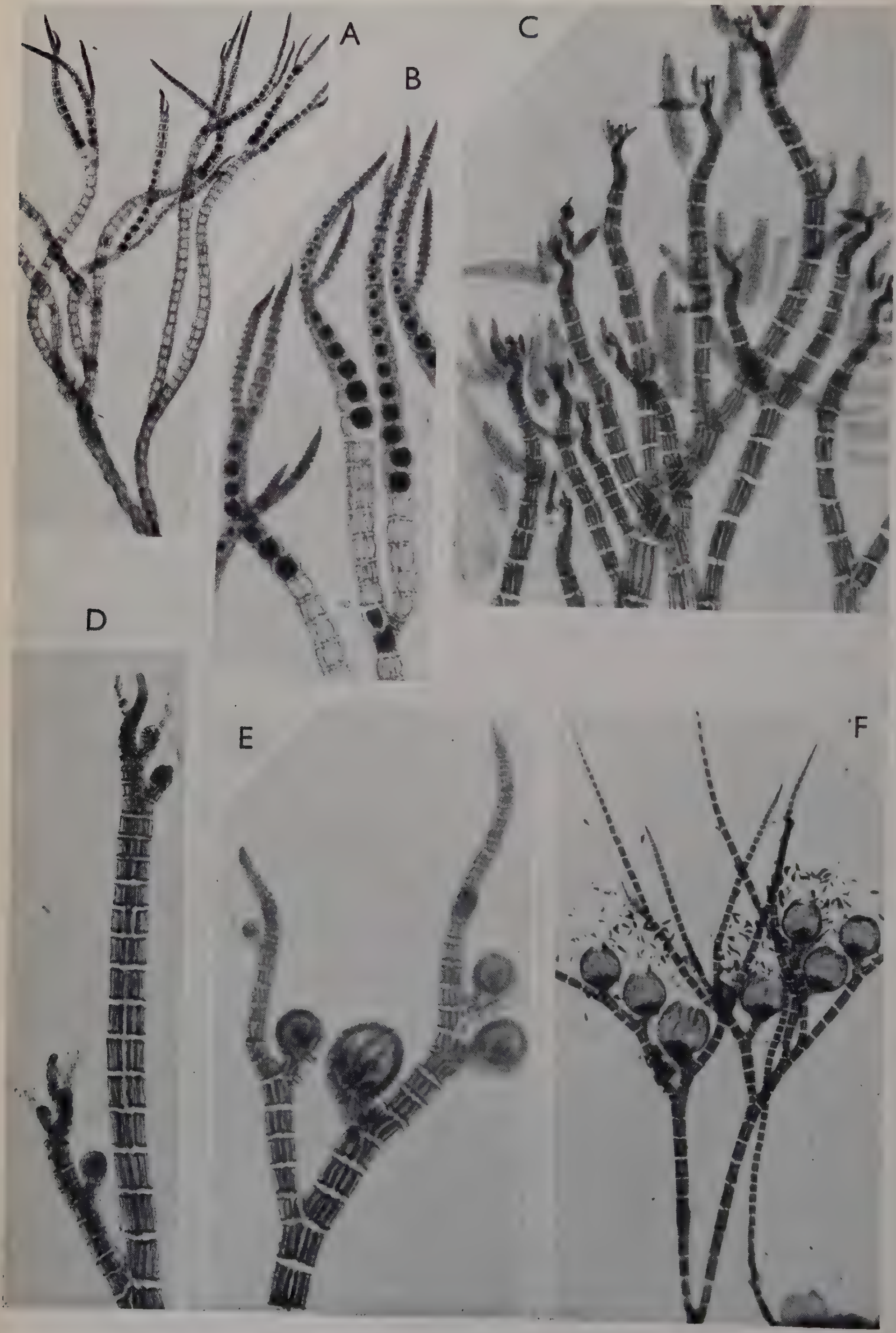
Rhodomelopsis africana



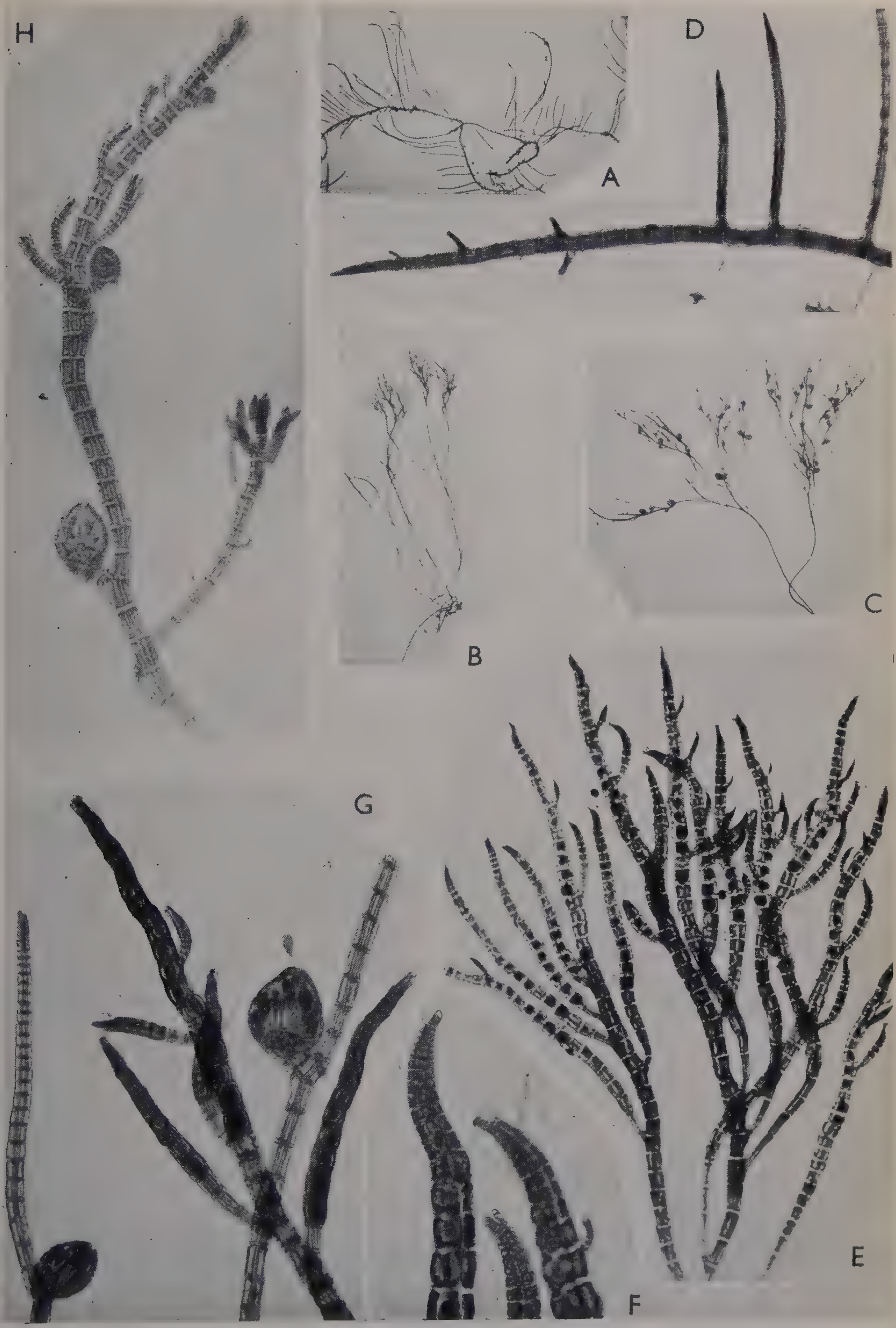
A–C. *Rhodomelopsis africana.* **D.** *Streblocladia tenuissima*



Placophora eckloniæ



Streblocladia tenuissima



Falkenbergiella caespitosa

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EXPLANATION OF PLATES 5–9

Plate 5.

Rhodomelopsis africana. A. Whole plant (Type) from Arniston. $\frac{2}{5}$ life size. B. Tip of tetrasporic plant showing general habit. × 20. C. Growing apex showing radial branching and absence of trichoblasts. × 94. D. Transverse section of young erect axis showing central cell, seven pericentral cells (crowded with rhodophycean starch) and two series of cortical cells. × 84. E. Cluster of tetrasporiferous branches showing stichidia in various stages of development. × 60. F. Older torulose stichidia, tetraspores mostly shed, showing contrast between nearly ecorticate stichidia and fully corticated branch. × 27.

Plate 6.

Rhodomelopsis africana. A. Apex of ♂ plant showing branchlets producing antheridial clusters. Mature clusters mostly shed. × 60. B. Apex of branch from ♀ plant showing three groups of procarp-bearing branchlets. × 78. C. Branches bearing nearly mature and immature cystocarps. × 20. *Streblocladia tenuissima.* D. Part of Type sheet. From Cove Rock. About $\frac{7}{12}$ life size.

Plate 7.

Placophora ecklonіae. A–D. Tetrasporic plants. A. General habit. × 3. B. Flat thallus with erect fertile branches in dense group behind growing margin. × 20. C. Well-grown plant showing production of lateral branchlets. × 20. D. Tip of fertile axis. × 78. E, F. Male plant. E. Fertile axes (antheridial clusters mostly shed) arising from thallus. × 20. F. Tip of male axis showing developing antheridial branchlets at apex, a single nearly mature cluster and projecting 'bearing cells' left by fallen clusters. × 210. G, H. Female plant. G. General habit. × 20. H. Nearly mature cystocarps. × 78.

Plate 8.

Streblocladia tenuissima. A, B. Tetrasporic plant. A. Part of apical cluster of fertile branches showing pseudodichotomous branching. × 20. B. Fertile branches further enlarged. × 48. C. Male plant. Part of a single apical tuft of fertile branches. × 335. D–F. Female plant. Apices of fertile shoots. D. Young cystocarps showing trichogynes, hair-bearing trichoblasts. × 335. E. Older cystocarps, trichoblasts shed. × 94. F. Mature cystocarps with extruded carpospores. × 20.

Plate 9.

Falkenbergiella caespitosa. A–C. General habit. All × 3. A. Young tetrasporic plant showing prostrate axes and erect unbranched axes, a few beginning to form tetraspores. B. Older tetrasporic plant with tufts of stichidia. C. Part of mature female plant with many cystocarps, of various ages. D. Apex of prostrate axis showing young branches and attachment organs. × 37. E, F. Tetrasporic plant. E. Part of tuft of stichidia borne by a single erect axis. × 27. F. Apices of young tetrasporic branches showing developing trichoblasts. × 86. G. Tetrasporic branches showing laterals and well-developed hyaline hairs and two branches from female plants with cystocarps, one young, the other mature. × 48. H. Hermaphrodite plant. Branch bearing young cystocarps, hair-bearing trichoblasts well developed, with lateral branch bearing antheridia-hyaline hairs notably absent. × 40.

South African parasitic Florideae and their hosts. 2. Some South African parasitic Florideae. By MARGARET T. MARTIN, Ph.D., F.L.S. and MARY A. POCOCK, Ph.D., F.L.S.

(With Plates **10–12** and 7 Text-figures)

[Read 4 January 1951]

From time to time various Floridean genera have been recorded and described as parasites upon other marine algae, generally other members of the Florideae. The earliest records were those of Reinsch (1875) for *Syringocolax* and for a number of species of *Choreocolax* from Europe and North America, and of Solms-Laubach (1877) for *Janczewskia* from the Mediterranean. A number were described either by Schmitz or Falkenberg in Engler & Prantl (1897), e.g. *Microcolax, Stromatocarpus, Chamaethamnion,* and some of them treated in more detail by Falkenberg (1901). Many of these records were from the southern hemisphere, i.e. Australia, New Zealand, the Auckland Islands, the Cape of Good Hope, while more recently the reports of various expeditions, e.g. Kylin & Skottsberg (1919), Weber van Bosse (1929), Levring (1941, 1944, 1945), Baardseth (1941), have added to their number. Since 1910, however, Setchell and his fellow-workers have recorded a number of parasitic Florideae from the Pacific coast of North America, and in the last few years Smith (1944) and Dawson (1944, 1945) have added others from the Californian coast. So far, comparatively few genera have been found in northern Europe: of these, *Choreocolax, Harveyella* and *Holmsella* are fairly well known through the work of Sturch (1899, 1926), and there are also records of *Gonimophyllum, Choreonema, Callocolax* and *Ceratocolax.*

In the course of collecting on the shores of South Africa from 1939 to 1948, a number of these parasites has been encountered, a few in the colder waters of the west coast, but more along the warmer south and south-east coasts. Only two of them have previously been recorded from South Africa; of the rest, some are new species belonging to genera known from other parts of the world, while others represent entirely new genera. In the present paper we intend to give a brief summary of those found, together with descriptions of the new genera and species; of these, certain show features of interest which it is hoped to treat more fully in subsequent papers. Some of the host plants, too, have proved to be new species or genera, and these are described separately (Pocock, 1953).

The numbers quoted refer to specimens in the herbarium of Dr M. A. Pocock.

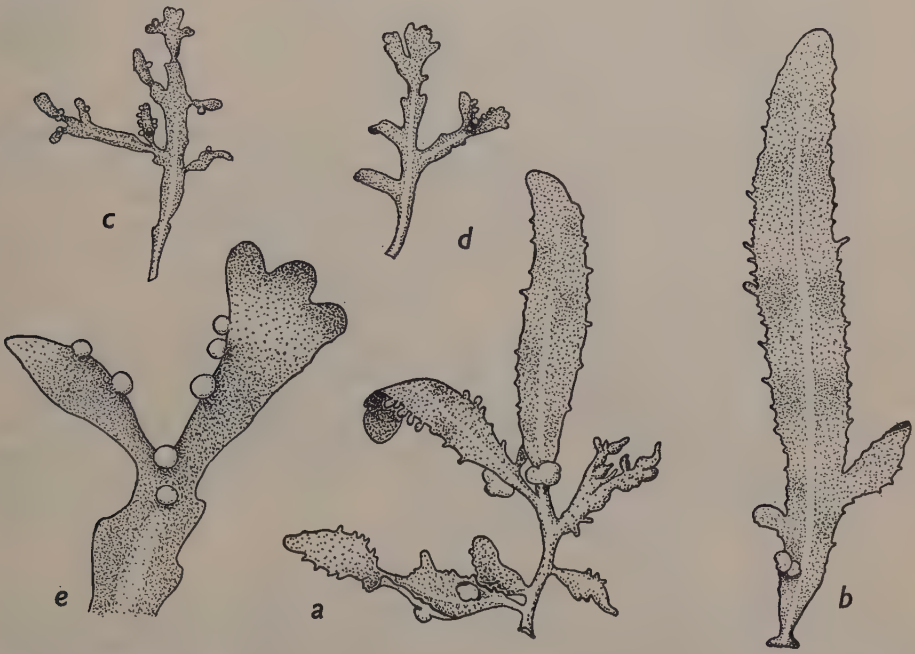
Choreocolax suhriae sp.nov.

Thallus parasiticus in frondibus *Suhriae vittatae* ad oras Capitis Peninsulae. Pustulae verrucae similes saepe in inferiore regione hospitis, plerumque pallidae aut rare magis rubrae, filamentis et parasiti et hospitis compositae. Spermatangia, cystocarpia et tetrasporangia in separatis pulvinulis, et ut in hoc genere.

Parasitic on *Suhria vittata* on the shores of the Cape Peninsula. Forming small wart-like swellings, often on the basal part of the host fronds, each pustule usually pale in colour, but sometimes deeper red, and composed of both parasite and host tissue. Spermatangia, cystocarps and tetrasporangia on separate pustules and characteristic of the genus.

Type specimen: 8335, from Blaauwberg, Dec. 3, 1944.

The host plant, *S. vittata*, is found on the coasts of the Cape Peninsula and occurs as an epiphyte, usually densely crowded on the stipes of the large 'Sea Bamboo', *Ecklonia maxima* Papenfuss. The parasite is not of very frequent occurrence, i.e. it has so far been common experience to examine about ten or twelve *Ecklonia* stipes before any of the *Suhria* plants are found to be infected; when it does occur, however, it has generally spread over a number of the host plants, forming small swellings which are especially frequent on or near the mid-rib in the lower part of the host frond and often actually on the short stipe at the base. In this position, the pustules are generally almost colourless when fresh, although further up the frond where the host tissues are deeply pigmented the parasite too may be darker in colour (Text-fig. 1 *a*, *b*). Obviously it is seldom possible to examine stipes of growing *Ecklonia* plants, hence *Choreocolax suhriae* has most often been obtained from plants cast up on the shore. It has, however, been collected from attached plants of *Ecklonia* growing in comparatively sheltered water at Blaauwberg, north of Table Bay, in July and December. It has been found in December and January in drift at Hout Bay and Kommetje, and in November at Maclear's Beach, all on the west coast of the Cape Peninsula, but is most frequent in False Bay at Strandfontein and Muizenberg where it has been collected repeatedly (January, March, September and December).



Text-fig. 1. *a*, *b*, fronds of *Suhria vittata* with pustules of *Choreocolax suhriae*. *c*, *d*, *e*, *Gelidium pinnatifidum*, narrow fronds from base of plant showing parasitic *Choreocolax margaritoides*. *a*–*d*, × 2; *e*, × 10.

The type species of the genus *Choreocolax* is *C. polysiphoniae*, parasitic on *Polysiphonia lanosa* (L.) Tandy and fully investigated by Sturch (1926). In this species the swellings are composed entirely of parasite tissue, apart from an odd pericentral cell of the Polysiphonia plant which becomes displaced and carried up with the parasite filaments. *C. suhriae* differs from the above in that the wart-like swellings are composed of a dense mixture of parasite filaments and host tissue, often causing some distortion of the host plant, and resulting in a much larger pustule which is often nearly as deeply pigmented as the host (Pl. **10** *a*, *b*). The difference in composition of the pustule may well be a result of the different thallus construction of the host; in *Suhria*, where the thallus is cellular with a hyphal medulla, the host tissue contributes to the formation of the pustule, while in *Polysiphonia*, with its narrow polysiphonous filaments, the host tissue is not involved.

In *Choreocolax suhriae*, the pustule eventually becomes covered with a clear, colourless zone composed entirely of cells of the parasite arranged in parallel rows and bearing the reproductive organs (Pl. **10** *a*, *b*). Tetrasporangia, spermatangia and carpogonia giving rise to cystocarps are found on separate pustules and seem to agree with those characteristic of the genus and described by Sturch. In the development of the cystocarp, however, there appear to be some differences in detail, and this feature needs fuller consideration.

Choreocolax margaritoides sp.nov.

Thallus parasiticus in frondibus *Gelidii pinnatifidi* in orientali regione orae Africae australis. Pulvinuli nitentes candidi, plerumque in frondibus angustis ex inferiori hospitis regione exeuntibus, filamentis parasiti omnino compositi. Spermatangia, cystocarpia et tetrasporangia in separatis pulvinulis, et ut in hoc genere.

Parasitic on *Gelidium pinnatifidum* on the south-east coast of South Africa. Forming small shining white pustules, generally on narrow fronds which grow out from the base of the host plant. Pustule composed entirely of parasite tissue; spermatangia, cystocarps and tetrasporangia on separate pustules and characteristic of the genus.

Type specimen: 6330, from Kleinemonde (East of Port Alfred) in drift, 27 September 1942.

This parasite has only been found on two occasions, once at Richmond, a little west of Port Alfred, and once at Kleinemonde, about 30 miles farther east, the two collections being made within a few weeks of each other (August and September 1942). The host plant was the large *G. pinnatifidum*, the infected region being the narrow fronds which grow out near the base of the plant (Text-fig. 1*c*, *d*), where the white colour of the parasite contrasts sharply with the deep red pigmentation of the host. The specific name of 'margaritoides' has been given to this parasite in reference to the pearly lustre of the tiny rounded pustules.

This species differs from *Choreocolax suhriae*, described above, and resembles the type species *C. polysiphoniae*, in that the pustule is composed entirely of parasite tissue, with rhizoidal filaments penetrating into the host below. The pustules are much smaller than those of *C. suhriae*, being barely visible to the naked eye, and appear to break out of the host tissue (Text-fig. 1*e*; Pl. **10***c–e*) sometimes on the flattened surface, but frequently at the margin of the narrow frond. Tetrasporangia, spermatangia and cystocarps resemble those described by Sturch for *C. polysiphoniae*.

Plocamiocolax papenfussiana sp.nov.

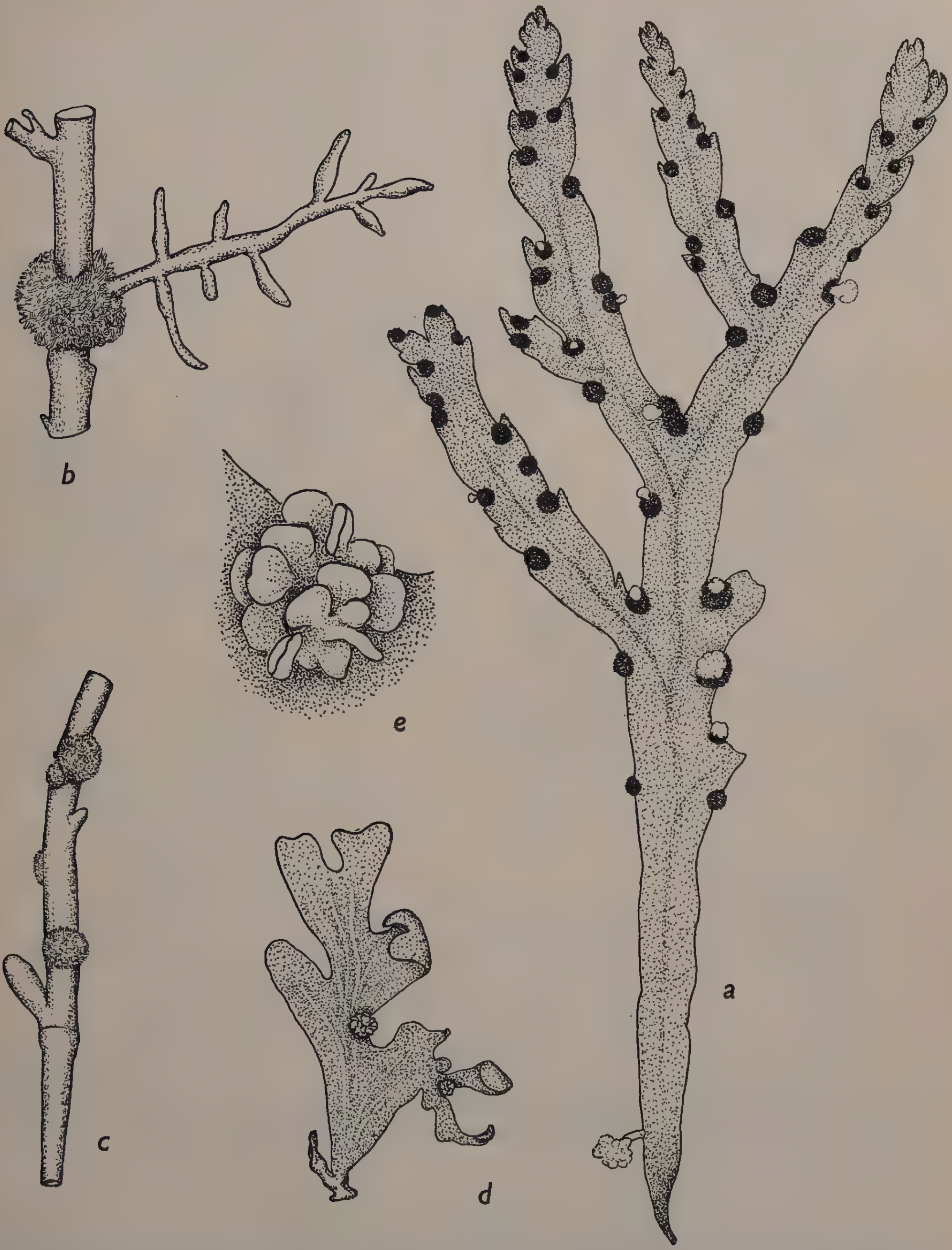
Thallus parasiticus in frondibus *Plocamii corallorhizae* ad oras australes et orientales Africae australis. Pulvini albi, saepe caulati, ex hospitis soris orientes aut rarius in margine aut regione frondis basali. Contextus hospitis filamentis tenuibus ramosis rhizoidalibus penetratur. Parasitus aut tetrasporicus brevibus stichidiis et tetrasporis albis aut sexualibus spermatangiis et carpogoniis in isdem ramis; haec formata ut in *Plocamio*.

Parasitic on *Plocamium corallorhiza* from the south and east coasts of South Africa. Forms white tufts, often stalked, arising from the sori of the host plant, or more rarely from the margin of the thallus or basal parts. Host tissue penetrated by fine branching rhizoidal filaments. Plants either tetrasporic, with stunted stichidia and colourless tetraspores, or sexual, bearing spermatangia and carpogonia on the same branches. Development of reproductive organs similar to *Plocamium*.

Type specimen: 8575, from Strandfontein, 5 January 1946.

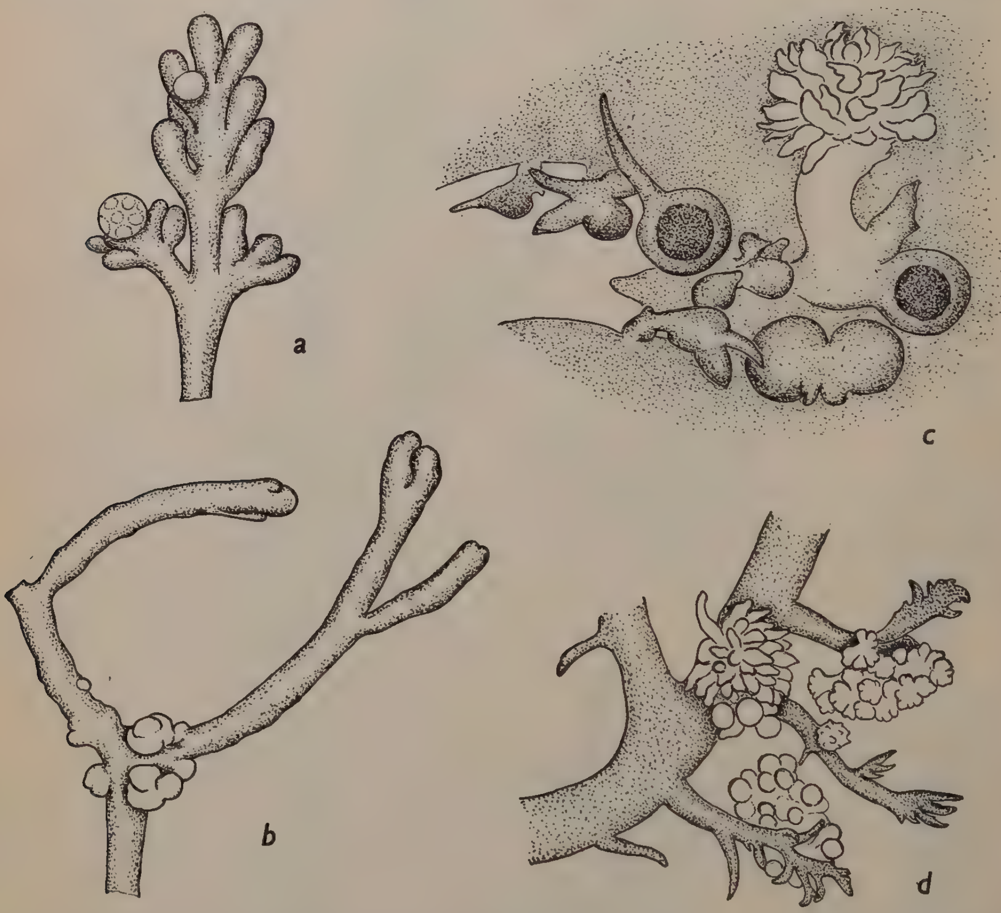
The host on which this parasite is found is a large South African species of *Plocamium*, *P. corallorhiza*, a species found along the south coast from Cape Point eastwards to East London and beyond. The parasite has been collected throughout the whole range occupied by the host plant, though the best material comes from Strandfontein, in False Bay, where it can be found at almost any time of the year, and can be collected on host plants *in situ* at low-water spring tide.

P. corallorhiza is a species of *Plocamium* with a wide flattened thallus, and reproductive sori borne in the marginal notches. The parasite appears as white tufts, generally arising from the sori of the host, and contrasting sharply with their deep red colour; occasionally,



Text-fig. 2. *a*, *Plocamium corallorhiza*, showing tetrasporic sori (dark) and parasitic *Plocamiocolax papenfussiana* (light). *b*, *c*, parts of frond of *Gelidium cartilagineum* with parasitic *Syringocolax macroblepharis*. *d*, *e*, *Acrosorium acrospermum* with *Gonimophyllum africanum*. *a*, nat. size; *b*, *c*, ×3; *d*, ×2; *e*, ×17.

however, specimens are found on the margin of the host frond or on the basal parts (Text-fig. 2*a*). Each parasite plant consists of a more or less elongated stalk-like portion, which may be as much as 5 mm. in length, and from which a number of irregular lumpy branches arise (Text-fig. 3*c*). Below the visible part of the parasite, the host tissue is penetrated by a mass of very fine branching rhizoidal filaments, which can frequently be seen making contact through pit connexions with the host cells.

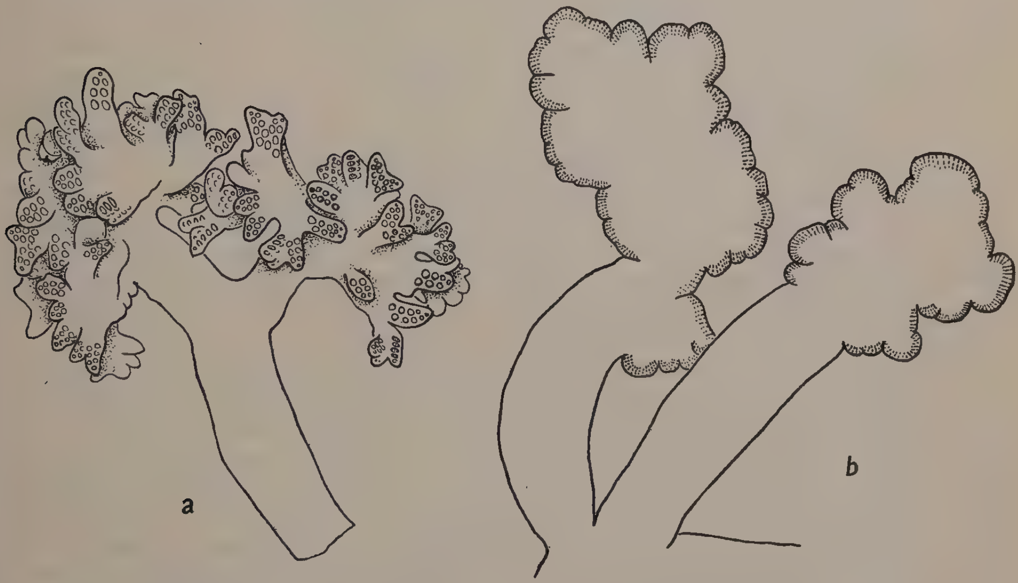


Text-fig. 3. *a*, *b*, pustules of *Janczewskia meridionalis* on *Laurencia flexuosa*. *c*, sexual plant of *Plocamiocolax papenfussiana* (white) growing from female sorus of *Plocamium corallorhiza*. *d*, sexual and tetrasporic plants of *Plocamiocolax pulvinata* growing on *Plocamium pacificum*. *a*, *b*, ×3; *c*, *d*, × 20.

Tetrasporic plants of the parasite resemble to a large extent the tetrasporic sori of the host; they are, however, quite devoid of pigment, and the stichidia are much more stunted and irregular in their branching. The tetraspores are produced in the same way, but are completely colourless. The parasite is monoecious, spermatangia and procarps being regularly found on the same branches of the sexual plants, an unusual feature in this group of the Florideae. Their development and structure is typically that of *Plocamium* (cf. Kylin, 1930).

It is hoped to describe and illustrate this parasite in more detail in a later paper. It is obviously closely allied to its host, *Plocamium*, and must be placed near to it. Setchell

(1923) has described a parasite on *P. coccineum*[1] from California and has named it *Plocamiocolax pulvinata*, but his account is confined to a Latin diagnosis and there are no figures. Prof. G. F. Papenfuss has, however, supplied me with excellent material of what appears to be the same parasite on *Plocamium pacificum* Kylin (Text-fig. 3*d*) and a comparison with this shows that the South African parasite should clearly be included in the genus *Plocamiocolax*. The resemblances between the Californian and the South African specimens are close, but in the Californian *P. pulvinata* there is an even greater reduction in the ultimate branching in the tetrasporic plants, so that the result is a much lobed and closely fastigiate mass in which the developing tetrasporangia are embedded. This is shown clearly in Text-fig. 4*a*, *b*. This appears to be a constant feature of difference, and considering it together with the difference of host and locality, it would seem best to refer the South African parasite to a new species which we have pleasure in naming *P. papenfussiana*, after Prof. G. F. Papenfuss who first drew our attention to it.



Text-fig. 4. *a*, *Plocamiocolax papenfussiana*. *b*, *Plocamiocolax pulvinata*, part of tetrasporic plants. × 40.

Syringocolax macroblepharis Reinsch.

[Lectotype: 8525, on *Gelidium cartilagineum* from East London, near Bats Cave, 23 September 1945.]

Syringocolax was first described and named by Reinsch (1875) as a monotypic genus, the one species, *S. macroblepharis*, being parasitic on *Gelidium cartilagineum*. Reinsch gives the locality as 'mare borealis', but this is obviously an error since at the same time he describes two other Florideae, *Alsidium adhaerens* and *Entocolax naegelianus*, as growing upon *Gelidium cartilagineum* from 'Cap Agulhas Africa meridionalis'. Specimens of all these are obviously from the same locality and probably all on the same material of *Gelidium*. De Toni quotes the distribution from Reinsch 'sine exacta indicatione loci' but Schmitz in Engler & Prantl gives the locality correctly as the south coast of Africa. The only accounts of *Syringocolax* are the three mentioned above, and the only figures those of Reinsch, which show the form of the parasite cushion, a few cells from the parasite and its penetration into the host tissue, and 'polysporangia', which are the only reproductive organs seen by this author, and presumably are the cystocarps. Schmitz and Hauptfleisch, in Engler & Prantl (1897), make brief mention of tetrasporangia, antheridia, procarps and cystocarps, but give no details or figures.

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[1] *P. coccineum* does not occur on the Californian coast, and Setchell's material is almost certainly to be referred to *P. pacificum*.

During the last few years, specimens of this parasite on *Gelidium cartilagineum* have been collected from a number of localities on the south coast of South Africa, extending from Cape Agulhas eastwards to Morgan Bay, near Kei Mouth. The host is a sublittoral form, and most of the specimens have been collected from material cast up as drift; the parasite forms compact pustules and is most frequently found on the long naked stipe-like region below the pinnate branching of the host frond (Text-fig. 2*b*, *c*). It may occur right at the base of the stipe near the attachment to the substratum and also on the upper part of the frond, though here it is always on the stem-like axis and never on the flattened leaf-like parts. The pustules have a velvety surface and are always pale in colour as contrasted with the deep red colour of the host; they are devoid of red pigment and practically colourless when found on attached plants of *Gelidium*, but have often become pinkish brown when found on drift specimens. This discoloration of the parasite is a very usual phenomenon in parasitic Florideae and is probably often caused by a leaching out of the pigment from the host cells into the parasite.

On a few occasions *Syringocolax* has been found parasitic on another species, *Gelidium amansii*, as host. So far, there do not appear to be any essential points of difference which would warrant the reference of these specimens to a distinct species, and what differences have been noted may well be attributable to differences in the habitat of the host. Whereas *G. cartilagineum* is characteristic of rock faces exposed to strong wave action, *G. amansii* is generally found growing on the floor of rocky bays between reefs, where the plants are more sheltered from wave action and not exposed at low tide. The parasite on these plants has longer filaments which often become branched at their tips, and altogether appears more luxuriant in habit.

The structure of the filaments of *Syringocolax* and the development of its reproductive organs are little known, and since they present several features of interest, it is proposed to treat them more fully in a later paper. For the present, figures are included which will show the gross features of organization (Pl. **11** *a–c*). It will be seen that the pustule is composed of a compact central region, made up of densely interwoven filaments, from which 'rhizoidal' filaments penetrate into the host tissue. From the surface of the pustule arise long, terete, radiating axes, at first unbranched, which bear the reproductive organs. Tetrasporangia are borne in vertical rows along the whole length of the fertile axis, the tetraspores being tetrahedrally arranged (Pl. **11** *c*). The male axis shows fertile areas, where the spermatangia are densely packed over the entire surface; it often has a sterile tip, and occasionally alternating sterile and fertile regions (Pl. **11** *a*). The procarps are borne in a vertical row along the female filament, with a parallel row of sterile hairs; after fertilization, a naked cystocarp develops, and protective branchlets grow out enveloping it in a loose cluster (Pl. **11** *b*). Both form and development of the cystocarp are characteristic of the Ceramiaceae.

Gonimophyllum africanum sp.nov.

In frondibus Delesseriacearum diversarum parasiticum ex Africa australi et praecipue in quibusdam Acrosorii speciebus. Simillimum *Gonimophyllo buffhami* Batters, sed thallus cystocarpicus minus complanatus et minus frondisimilis. Organa reproductionis characteres generis habent.

Parasitic on various Delesseriaceae from South Africa, and especially on *Acrosorium* spp. Very similar to *Gonimophyllum buffhami* Batters, but female plants show branches which are less flattened and leaf-like. Reproductive organs characteristic of the genus.

Type specimen: 9138, on *Acrosorium maculatum*, from Cove Rock, near East London, 20 July 1947.

The genus *Gonimophyllum* was founded by Batters (1892), and the species *G. buffhami* described from material collected at Deal, on the south coast of England, as a parasite on *Nitophyllum laceratum* (now = *Cryptopleura ramosa* Kylin). In later years this parasite has been found in other localities in Britain, and we have recently found it quite frequently on *Cryptopleura ramosa* on the Anglesey coast. Two further species have been described, *Gonimophyllum australe* Skottsberg, from the Falkland Islands, which has since been transferred to a new genus, *Gonimocolax* Kylin (1924); and *G. skottsbergii* Setchell from California, found parasitic on several Delesseriaceae and differing from the other two species in having polysporangia containing from thirty to fifty polyspores.

The South African species has been collected on a variety of hosts, all members of the Delesseriaceae, e.g. *Botryoglossum platycarpum*, *Neuroglossum binderi*, *Botryocarpa prolifera*, but most frequently on several species of *Acrosorium*, including *A. acrospermum* Kylin and a maculate, uncinate species, probably a variety of *A. uncinatum*. The material described here was collected on *Acrosorium acrospermum* from Kleinemonde near Port Alfred, but specimens have also been obtained from Woodstock in Table Bay, from Cape Agulhas, and as far east as Morgan Bay near Kei Mouth. It has been collected in January, February, July and December, and appears to be fertile at all these times of year. Ripe cystocarps, however, have not yet been seen.

In appearance, the plants are very similar to those of *G. buffhami* recently examined from Anglesey. They consist of a basal cushion, formed by the division of the host cells to form rows of cells flattened horizontally and interspersed with small branching monosiphonous filaments of the parasite. From the surface of the cushion arise the fertile laminae, male, female and tetrasporic on separate cushions (Text-fig. 2*d*, *e*). The laminae are less obviously stalked than those figured by Buffham, and are often considerably lobed; the male and tetrasporic are flattened and often bifurcately lobed at the tip. Tetrasporangia are scattered irregularly over the central part of both surfaces, the tetraspores being tetrahedrally arranged. The male fronds are fertile over nearly the whole area on both surfaces, except for a narrow sterile margin and the basal 'stalk'. Both male and tetrasporic fronds very closely resemble those of *G. buffhami* from Anglesey. The female fronds, however, are narrower and less flattened; carpogonial branches are scattered over the frond, and the developing cystocarps project as rounded lobes from the surface.

The main difference from the Anglesey specimen is thus in the less flattened and leaf-like female frond; this difference is perhaps a small one, but taken in conjunction with the different locality and hosts suggests that the South African plant is better referred to a new species, *G. africanum*. It is hoped to examine these two species further now that abundant material of *G. buffhami* is available, and to treat them together more fully at a later date.

Stromatocarpus parasiticus Falk.

[Lectotype: 8187, on *Tayloriella virgata*, from Blaauwberg, 23 July 1944.]

This parasite was first described by Falkenberg (in Engler & Prantl, 1897) on *Polysiphonia virgata* (now *Tayloriella virgata* (Falk.) Papenfuss) from the Cape of Good Hope. In 1901, Falkenberg described it more fully with several figures illustrating especially the development of the tetrasporic stichidia.

We have collected material of *Stromatocarpus parasiticus* on *Tayloriella virgata* from a number of localities along the west coast of the Cape Peninsula, from Woodstock on the east side of Table Bay and from Blaauwberg farther north, where the infected host plant has been obtained in quantity from *Ecklonias* actually growing on the reef. It is common on the stipes of *Ecklonia* thrown up on the beaches and has been collected frequently at Hout Bay and Maclear's Beach on the west coast and at Strandfontein and Muizenberg in False Bay. Fertile material of the parasite has been found in both winter (June and July) and summer months (December to March).

Young plants of *Tayloriella* may often be found studded with small glistening hyaline pustules of *Stromatocarpus parasiticus*; on several occasions, however, the parasite was found to have spread to the erect fertile branches of *Placophora eckloniae* Pocock (1953) which sometimes forms a dense covering on the stipes of *Ecklonia*, usually associated with *Tayloriella*. Material on this host was first collected at Muizenberg in January 1944 and again in March 1948: it has also been found at Maclear's Beach and Hout Bay. Although these plants are somewhat smaller, this may well be attributed to the very much smaller host plant, and we see no reason to give them separate specific rank. When this parasite was first found on *Placophora*, the original host, *Tayloriella*, was represented only by the bases of old plants; it appears therefore as though the parasite may use *Placophora* as an alternative host.

Pl. **11** *d* shows the general appearance of *Stromatocarpus parasiticus* on *Tayloriella* and there is little to add to Falkenberg's description of its habit and reproductive organs. It should be mentioned, however, that Falkenberg writes of the basal monosiphonous part of the thallus running endophytically between the cells of the host plant, and Levring (1941) also describes the basal filaments of *Stromatocarpus microscopicus* as penetrating into the host plant and developing endophytically. Neither of these authors, nor Setchell (1923) for *S. gardneri*, makes any mention of actual parasitism of the host. In the material which we have examined, however, the parasite filaments penetrate the host tissue until they reach the cells of the central siphon; they wrap round this, and can clearly be seen making actual contact by means of pit connexions. This is one of the clearest and most striking cases of parasitism as yet seen in these Florideae, and is readily visible in almost any material examined of *S. parasiticus*.

Microcolax africana sp.nov.

Frons parasitica floccos ramosos in hospite faciens; rami vegetativi cum cellulis pericentralibus 4 et raris cellulis corticem in inferiore regione facientibus; non multum dorsiventralis sed aliter characteres generis habet; spermatangia et cystocarpia ut in hoc genere. Stichidia non complanata et plerumque una solum serie cellularum pericentralium fructiferarum; rare cellula pericentralis in serie proxima sporangium fert.

In frondibus *Streblocladiae tenuissimae* Pocock e Cove Rock prope East London, Africae australis.

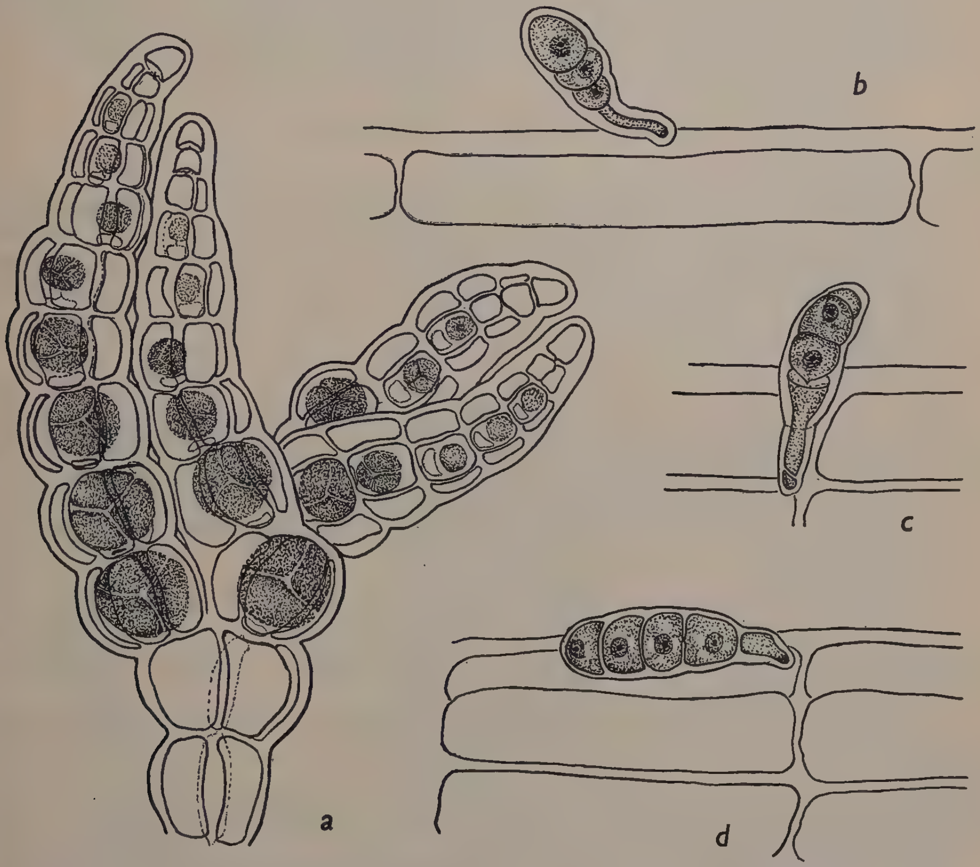
Parasitic, forming branched tufts on host; vegetative filaments with four pericentral cells and occasional corticating cells near base; only slightly dorsiventral, but otherwise characters those of genus. Spermatangia, carpogonial branches and cystocarps also typical of genus. Stichidia not flattened and generally with only one row of fertile pericentral cells, though occasionally a pericentral cell in adjacent row produces a sporangium.

Habitat. On *Streblocladia tenuissima* Pocock, from Cove Rock near East London, South Africa.

Type specimen: 7310, from Cove Rock, 18 July 1943.

The genus *Microcolax* was first described by Schmitz (in Engler & Prantl, 1897) with the single species *M. botryocarpa*. This plant had been previously recorded from Akaroa, New Zealand, and from the Auckland Islands by Hooker (1844) who, however, had mistaken it for the reproductive organs of the host plant which they therefore named *Polysiphonia botryocarpa*. Subsequently, Schmitz recognized that two plants were involved and separated the parasite as *Microcolax botryocarpa* and the host as *Streblocladia neglecta*. The structure is fairly well known from descriptions by Schmitz (*loc. cit*) and Falkenberg (1901). More recently, Levring (1945) has recorded specimens from the Auckland Islands and Campbell Islands and has amplified the original description of the development of the carpogonial branch and cystocarp.

The plant found in South Africa, and here described, is parasitic upon a small species of *Streblocladia* which has been named *S. tenuissima* (Pocock, 1953). The host plant probably occurs in a number of places on the coast of the south-east Cape Province, but has only been found with the parasite in one locality, Cove Rock, a few miles west of East London. When mature the parasite appears as small spherical excrescences on the slender red filaments of the host plant; when examined microscopically it is seen to consist of short branched axes radiating from the surface of the *Streblocladia*, to which it is attached by a system of rhizoidal branches; these penetrate the host tissue and may run along for some distance beneath the surface. The free axes are shortly stalked and richly branched above; they constitute the whole of the external body of the parasite, no cushion external to the host being formed (Pl. **12** *a–c*).



Text-fig. 5. *Microcolax africana*. *a*, Tetrasporic stichidia. *b*, *c*, *d*, germinating sporelings on *Streblocladia tenuissima*. *a*, ×280; *b–d*, ×370.

The free branches have four pericentral cells and show very occasional odd cortical cells near the base. The construction of the plant and the development of male and female reproductive organs agree closely with those described by Falkenberg (1901) and Levring (1945). In the organization of the stichidia, however, there is a striking difference. According to the diagnosis (de Toni, 1903) of the genus, the tetrasporangia, though one per segment, are arranged in two alternating rows: 'tetrasporangia secus duas lineas marginales alternantes disposita foventia', and Falkenberg's figures show very clearly these two rows of alternating tetrasporangia running along the outer margin of the curved and flattened stichidium.

The tetrasporangia in the present species are apparently arranged in a single row along the stichidium, which shows no sign of flattening, and at first sight this seemed to raise doubt as to inclusion within the genus *Microcolax*. A comparison with Levring's figures (1945), however, shows that in the material described by this author and attributed to *M. botryocarpa* there is no appreciable flattening of the stichidium, although the arrangement of the tetrasporangia is apparently alternate, and they arise from the two rows of pericentrals on the exterior side of the curved stichidium. Reference to the present species shows moreover that, although the sporangia are generally derived from only one of these rows of pericentrals, it is possible to find an occasional tetrasporangium developed from the adjacent row (Text-fig. 5*a*); this would seem to indicate that both rows of pericentral cells are potentially fertile, though here the fertility is generally restricted to one of them. It therefore seems best to retain the present plant in the genus *Microcolax*, and, having regard to this feature of the tetrasporangia, to the lesser degree of dorsiventrality, and to the different species of host, to refer it to a new species, *Microcolax africana*.

Melanocolax velutina gen. et spec.nov.

Melanocolax gen.nov.

Planta parasitica, pustulas faciens quae recentes pallidae servatae autem cito suffuscae fiunt. Filamenta monosiphonia contextum hospitis penetrant; rami fertiles liberi, a pulvino in exteriore parte hospitis crescentes. Ramulus masculus cylindratus ramum brevem monosiphonium terminans; ramus femineus cum segmentis polysiphoniis 4 aut 5 infra et monosiphoniis 3 aut 4 supra segmentum fertile; cystocarpia permagna. Tetrasporangia bina segmentis, raro decussata, plerumque superposita; tetrasporangia triangule divisa.

Parasitic, forming pustules which are pale when fresh and darken rapidly on keeping. Monosiphonous filaments penetrate host tissue; fertile branches free, radiating from a cushion external to the host. Male branchlet cylindrical, terminating short monosiphonous branch; female axis with 4 or 5 polysiphonous segments below and 3 or 4 monosiphonous ones above the fertile one; cystocarp very large. Tetrasporangia 2 per segment, occasionally decussate, but generally superposed: tetraspores tetrahedral.

M. velutina sp.nov.

Pustulae velutinae in hospite: pulvinus permagnus et densus: rami liberi cum cellulis pericentralibus 4. Cystocarpium permagnum, supra pulvinum sublatum: carposporia parva, ostiolium in summo.

In frondibus *Rhodomelopsidis africanae* Pocock e parte orientali orae australis Provinciae Capitis.

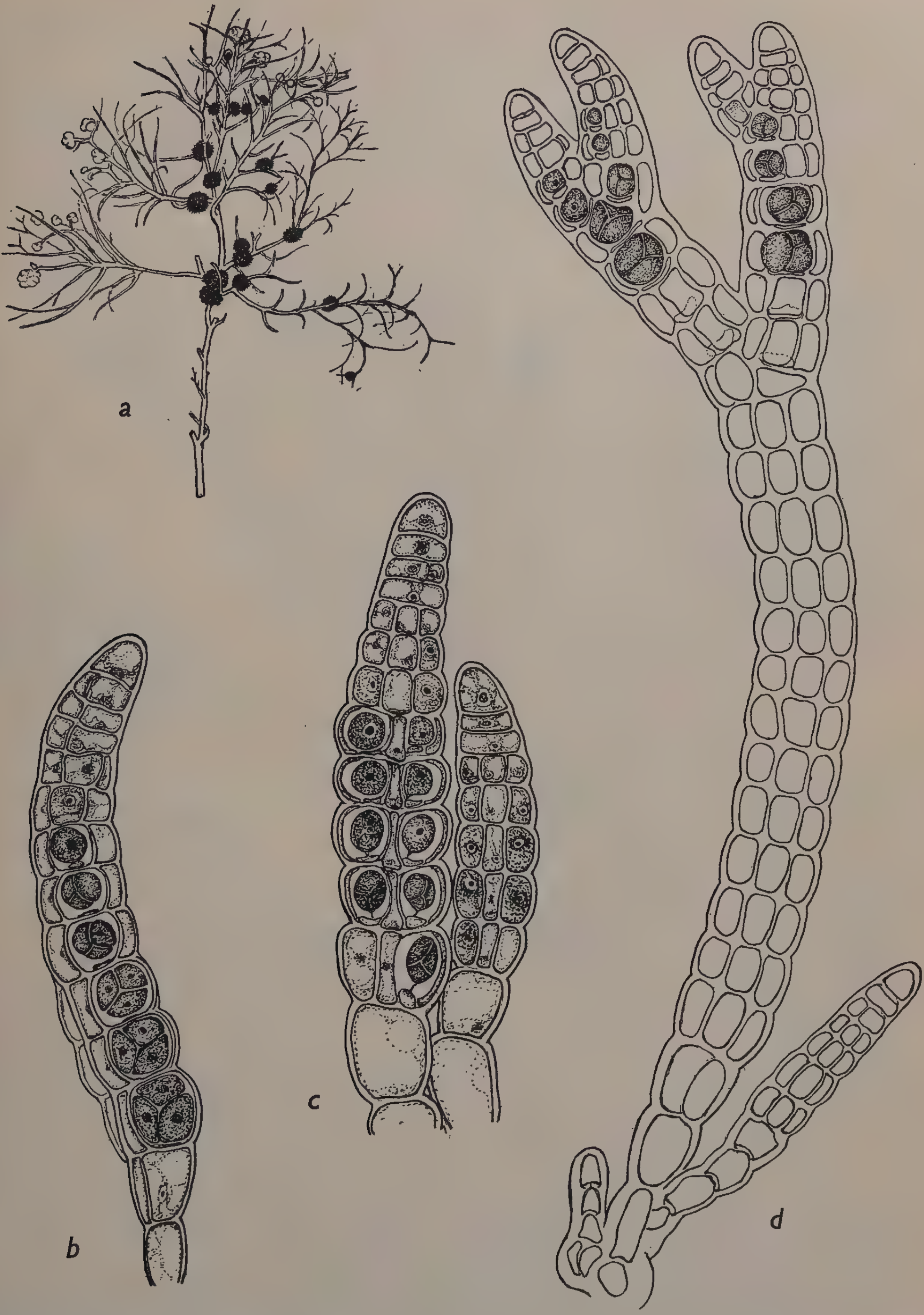
Velvety pustules on host plant; very conspicuous and compact external cushion: free branches with 4 pericentral cells. Cystocarp very large and raised above the surface of the cushion; carpospores small, ostiole terminal.

Parasitic on *Rhodomelopsis africana* Pocock, from south-east coast of the Cape Province.

Type specimen: 8784, from Riet River, the Three Sisters, 13 August 1946.

The host plant *R. africana*, on which this parasite occurs, is found along the south-east coast of the Cape Province, and material bearing the parasite has been collected from a number of localities from Arniston, just east of Cape Agulhas, to East London, being particularly abundant at Riet River, a few miles east of Port Alfred. Fertile material has been collected during nearly all months of the year.

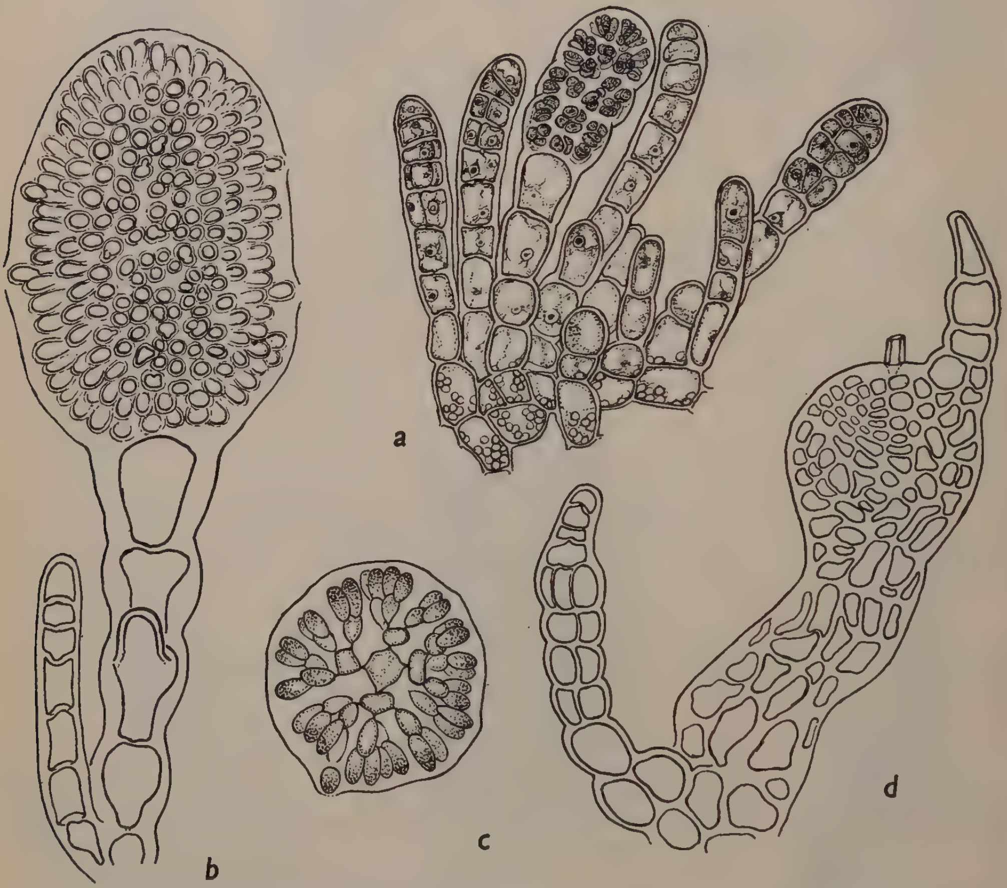
The parasite can be seen with the naked eye as a small cushion, often hemispherical but sometimes irregular in shape, and formed by the coalescence of several pustules which have evidently burst through the surface of the host at different points; adjacent pustules may sometimes be of different sorts, e.g. male and tetrasporic, and in such cases are evidently the results of separate infections. They are more frequently found on the lower parts of the host plant, but may also occur on its upper branches (Text-fig. 6*a*). They can be distinguished from the galls which also occur on the host by their softer



Text-fig. 6. *Melanocolax velutina*. *a*, pustules (dark) on plant of *Rhodomelopsis africana*, which also shows galls (light). *b*, *c*, stichidia in side and front view. *d*, older stichidium branched at tip, lower part empty of tetraspores. Cover cells are omitted for clarity. *a*, approx. nat. size; *b*–*d*, × 280.

consistency and the characteristic velvety appearance of their surface, due, as will be seen later, to the projecting tips of the closely packed fertile branches; when collected fresh they are almost unpigmented, but darken very rapidly on keeping.

One of the most striking characters of this parasite is the very well-developed cushion external to the host plant. It is composed of closely interwoven monosiphonous filaments which produce a compact, pseudo-parenchymatous structure, the cells being densely packed with starch (Text-fig. 7*a*; Pl. **12***f*); haustorial filaments penetrate between the host cells, wrap around cells of the central siphon and communicate with them by means of pit connexions. The erect branches produced from the surface of the cushion are short, generally simple, and merely serve to bear the reproductive organs.



Text-fig. 7. *Melanocolax velutina*. *a–c*, male branches. *a*, young stages; *b*, mature male branch; *c*, same in section. *d*, female, young fertile segment on left, developing cystocarp on right. *a*, *d*, × 280; *b*, *c*, × 480.

In the tetrasporic plant the free branches become almost entirely transformed for the purpose of bearing spores; generally two basal segments remain monosiphonous, and the rest cut off four pericentral cells each. Two sporangia are borne in each segment in opposite pericentrals, and successive pairs of sporangia are generally superposed (Text-fig. 6*b*, *c*); this is not invariable, however, and a decussate arrangement is sometimes seen, either in part or the whole of a stichidium. Often, too, only one sporangium develops in each of the one or two segments at the base of the fertile region. Two cover cells, a stalk cell and a tetrasporangium mother cell are produced from each fertile pericentral, and the tetraspores are tetrahedrally arranged. The apical cell remains active and the stichidium continues to grow in length while tetraspores are maturing and being liberated in the lower part; later it may branch once or more at the tip, in which case the older stichidium shows a long unbranched region empty of tetraspores, and several fertile branches at the tip (Text-fig. 6*d*).

In the female pustules the erect axis cuts off four pericentral cells from each segment in the basal region; the fourth or fifth segment from the base produces the carpogonial branch, and here five pericentrals are cut off. Above this the filament remains monosiphonous, so that there is a three- or four-celled sterile tip above the developing cystocarp (Text-fig. 7*d*). This suggests the trichoblast on which the sexual organs are commonly borne in the Rhodomelaceae. The trichoblast is a lateral branch; generally the two basal segments are polysiphonous, and the uppermost of these two is the fertile one (e.g. in *Polysiphonia*). In *Melanocolax*, although the fertile axes appear terminal, there is occasional sparse branching just at their base (Text-fig. 7*d*), and it is possible to imagine that, with the formation of a compact cushion, the main axis is much reduced, and the fertile axes may represent lateral branches of trichoblast nature. The fertile segment is here the fourth or fifth from the base, and in *Rhodomela virgata* it is generally the fourth. Here, of course, there is a biological advantage in that the resulting cystocarp is raised well above the surface of the cushion. Its development is apparently typical of the Rhodomelaceae, as seen in *Polysiphonia* or *Rhodomela*; the wall forms very early, before fertilization, and the mature cystocarp is spherical and very large, being raised above the cushion on a stout stalk, formed by the cutting off of cortical cells from the pericentrals of the lower segments (Pl. **12***f*). Numerous rather small carpospores are borne on a central placenta, and there is a terminal ostiole.

The free branches of the male plant remain monosiphonous below, while the upper four or five segments become fertile and each cuts off four pericentral cells; these produce the spermatangium mother cells and spermatangia. A terminal cylindrical body is thus formed, the surface of which is covered with spermatangia; its form and position are very similar to *Polysiphonia* and here, too, the fertile branch may represent an unbranched trichoblast (Pl. **12***e*; Text-fig. 7*a–c*).

As far as can be ascertained, no parasite of this form has been described before. The structure and development of the reproductive organs obviously place it in the Rhodomelaceae; the very large cystocarp suggests *Stromatocarpus*, and the well-developed basal cushion with its starch-containing cells is very similar to that described by Setchell (1923) for *S. gardneri*, material of which has been sent me by Prof. G. F. Papenfuss. At first it was thought that the parasite might be an extremely reduced species of *Stromatocarpus*, with unbranched erect filaments and a very compact basal cushion. Further consideration, however, seems to emphasize the points of difference from *Stromatocarpus*. All three species of *Stromatocarpus* so far described have slender and abundantly branched filaments (*S. parasiticus* Falkenberg (1901), *S. gardneri* Setchell (1923) and *S. microscopicus* Levring (1941)), while the erect filaments of this plant are almost unbranched; in *S. gardneri* and *S. microscopicus* there is a single row of sporangia in the stichidium, and in *S. parasiticus* a peculiar stichidium, resulting in four rows of sporangia, only one emanating from each segment, while in the parasite under consideration there are regularly two sporangia per segment, generally superposed. The cystocarp, too, is of very different form, being spherical with a stout stalk and wall and a minute ostiole, while the small carpospores radiate from a central placenta; mature cystocarps of *S. gardneri* are not available, but in the other two species the cystocarp is pear-shaped, with a well-marked ostiole, and a thin wall developing relatively late, the much larger carpospores being arranged on a flattened placenta.

On the whole, therefore, it seems best to regard this parasite as representative of a new genus. The cystocarp shows some similarity to that of the host, *Rhodomelopsis africana*, but in that plant the tetraspores are only one per segment. The two tetraspores per segment and the monosiphonous base of the stichidium suggest that *Melanocolax* might best be placed in the subfamily Pachychaeteae, where, too, the cystocarp may be massive and spherical in shape, but a more detailed study of the members of that group and of the parasite itself is needed before it is possible to determine with certainty its exact position among the Rhodomelaceae. Since one of its most obvious characters is the rapid darkening after collecting, we have named it *Melanocolax*, and, with reference to its soft velvety surface, *M. velutina*.

Janczewskia meridionalis sp.nov.

Pustulas parvas rotundas faciens, paululum bulbosa, sed nullis ramis liberis: color translucidus albidus. Organa sexualia et tetrasporangia omnia demersa in conceptaculis; antheridia in imo et lateribus conceptaculi masculi. E cystocarpiis crescentibus bulbi fiunt in thallo; tetrasporangia in superficie conceptaculi, tetrasporangia triangule divisa. In frondibus *Laurenciae flexuosae* et aliarum specierum *Laurenciae* e parte orientali orae australis Provinciae Capitis.

Forming small spherical pustules, somewhat lobed, but with no free branches; a translucent whitish colour. Sexual organs and tetrasporangia all sunken in conceptacles; male showing antheridial tufts which line the base and sides of the conceptacle; development of cystocarps results in globular lobes to the thallus; tetrasporangia lining the conceptacle, tetraspores tetrahedral.

Parasitic on *Laurencia flexuosa* and other species of *Laurencia* from the south-east Cape Province.

Type specimen: 8680, on *Laurencia flexuosa* from Riet River, 16 June 1946.

Janczewskia was the first parasitic red alga to be at all fully described, the genus being founded by Solms-Laubach (1877) with the type species *J. verrucaeformis* from the Mediterranean. Falkenberg later (1901) published an extended account of the genus, and mentioned a species on a *Laurencia* from South Africa, being doubtful whether or not it should be referred to *Janczewskia verrucaeformis*. Setchell (1914) described and figured six species from the coast of California including *J. verrucaeformis*, all parasitic on species of *Laurencia* or *Chondria*.

Specimens of *Janczewskia* have been found on host plants of five or six species of *Laurencia* on the south and east coast of South Africa, from Cape Agulhas eastwards and as far north as St Lucia Bay. Some of these species of *Laurencia* have not yet been identified, but at least two of them, *L. flexuosa* and *L. natalensis*, are well-known species. It seems probable that the specimens of *Janczewskia* will all prove to belong to the same species; for the present, the description is based on the specimens growing on *L. flexuosa*, and collected at or near Port Alfred.

The parasite forms translucent lumps on the upper parts of the fronds of *Laurencia flexuosa* (Text-fig. 3*a*, *b*). These may remain spherical or become slightly lobed; on the female, the ripening cystocarps cause a number of swellings on the surface. Apart from these, the plant never shows any free branches, and corresponds to Setchell's subsection *Eu-Janczewskia*, to which he refers two species, *J. verrucaeformis* and *J. solmsii*. Of these two, the present species resembles much more closely *J. solmsii*; both are entirely lacking in pigment, show little differentiation between host and parasite cells, and have their tetrasporangia developed in conceptacles, a character shown by no other known species. On the other hand, the South African plant differs from *J. solmsii* in several characters; the antheridial tufts spread much further up the sides of the conceptacle than in *J. solmsii*, and each of the tufts has a swollen basal cell as figured by Setchell for *J. verrucaeformis*. These characters, together with the different locality and host (*J. solmsii* is only known on the Californian species *L. subopposita*), suggest that the parasite should be referred to a new species, to which we have given the name *J. meridionalis*.

CONCLUSION AND SUMMARY

Descriptions have been given above of nine species of parasitic Florideae. Of these, two have been described before, six are new species, and one is an entirely new genus, while three of the hosts on which they grow have been referred to new species and are described in a separate paper in this *Journal* (Pocock, 1953). Consideration of these parasites raises several general points of which brief mention may now be made.

Most of the parasites are specific as regards their hosts. Of the nine considered here, there are only three exceptions to this: *Syringocolax macroblepharis*, which has been found occasionally on a second species of *Gelidium*; *Stromatocarpus parasiticus*, which spreads to an adjacent host (also a member of the same family, the Rhodomelaceae) when its normal one is undergoing a seasonal period of poor development; and *Janczewskia meridionalis*, which seems, unlike the species described from California, to occur on several species of *Laurencia*. In addition, the parasites often show a close systematic relationship to their hosts. Of the nine described here, only three do not belong to the same family as their respective host plants: i.e. the two species of *Choreocolax* and *Syringocolax macroblepharis*, all of which occur on species of *Gelidium*. This feature, together with the high degree of specificity, suggests that there is a close similarity between the metabolic products which makes those of the host easily utilizable by the parasite.

There are several features, shown to some degree by all these plants, which point undoubtedly to the relationship with their hosts being a parasitic one. In all of them the red pigment is much reduced or entirely lacking, and there is often a very sharp contrast in colour between the white shining parasite and its host; this is seen most strikingly in *Plocamiocolax* and in *Choreocolax margaritoides*. All of them, too, show considerable reduction in size compared with the nearly related host plants, some (e.g. *C. margaritoides*) being scarcely visible to the naked eye, and few forming pustules of more than 5 mm. in diameter. The vegetative thallus is generally much reduced, often to a system of branched haustorial filaments within the host. Sometimes, e.g. *Syringocolax* and *Melanocolax*, there is a well-developed cushion outside the host, packed with starch and utilized for storage, but in most the free axes are almost entirely reproductive, a state which is well seen in forms like *Microcolax africana*. Finally, there is abundant evidence of direct connexion between the haustorial system of the parasite and the host cells. The sporeling of the parasite germinates on the surface of the host and puts in a rhizoidal filament, as is shown for *Microcolax africana* in Text-fig. 5*b–d*; later, numbers of these can be seen spreading out fanwise in the host thallus, or in polysiphonous forms wrapping round the central siphon of the host. Wide pit connexions with the host can easily be seen, and there is some evidence that the closing membrane eventually breaks down.

There seems, then, no doubt at all as to the parasitic nature of these algae. The effect on the host, however, does not seem to be appreciable. In a few cases, e.g. in *Choreocolax suhriae* on *Suhria vittata*, there is some slight local swelling and distortion of the host tissues, and in *Gonimophyllum* there is some stimulation of the cell layers of the host to divide; any effect, however, seems to be a purely local one, and does not seem, so far as is evident at present, to affect the vigour or longevity of the host plant.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES 10–12

Plate 10

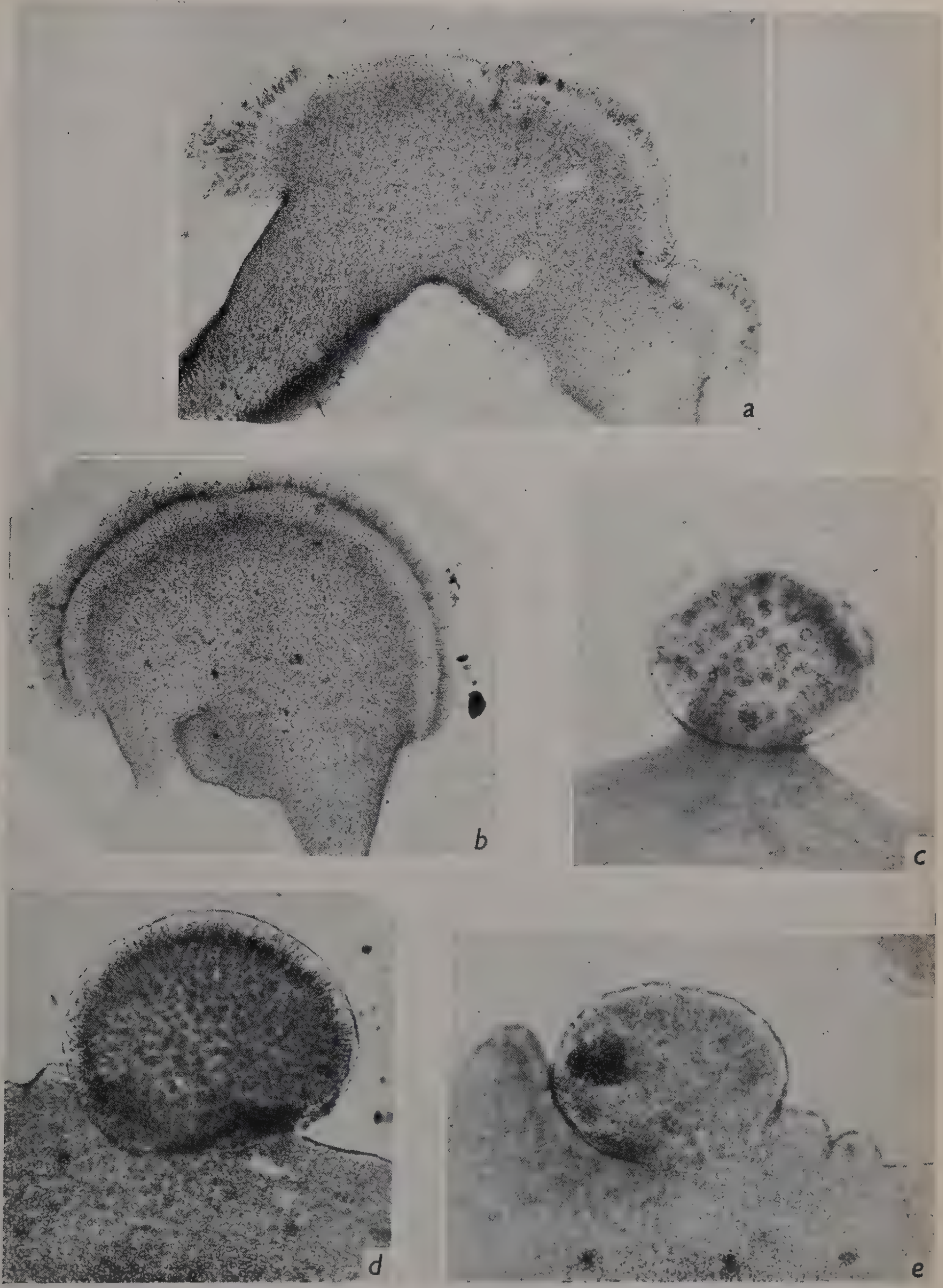
a, *b*, *Choreocolax suhriae*, vertical section through pustule on *Suhria vittata*; *a*, tetrasporic, *b*, male. *c–e*, pustules of *Choreocolax margaritoides* on *Gelidium pinnatifidum*: *c*, tetrasporic; *d*, male; *e*, female. In *e* note developing cystocarp (dark) and two young pustules on right. *a*, *b*, × 50; *c–e*, × 140.

Plate 11

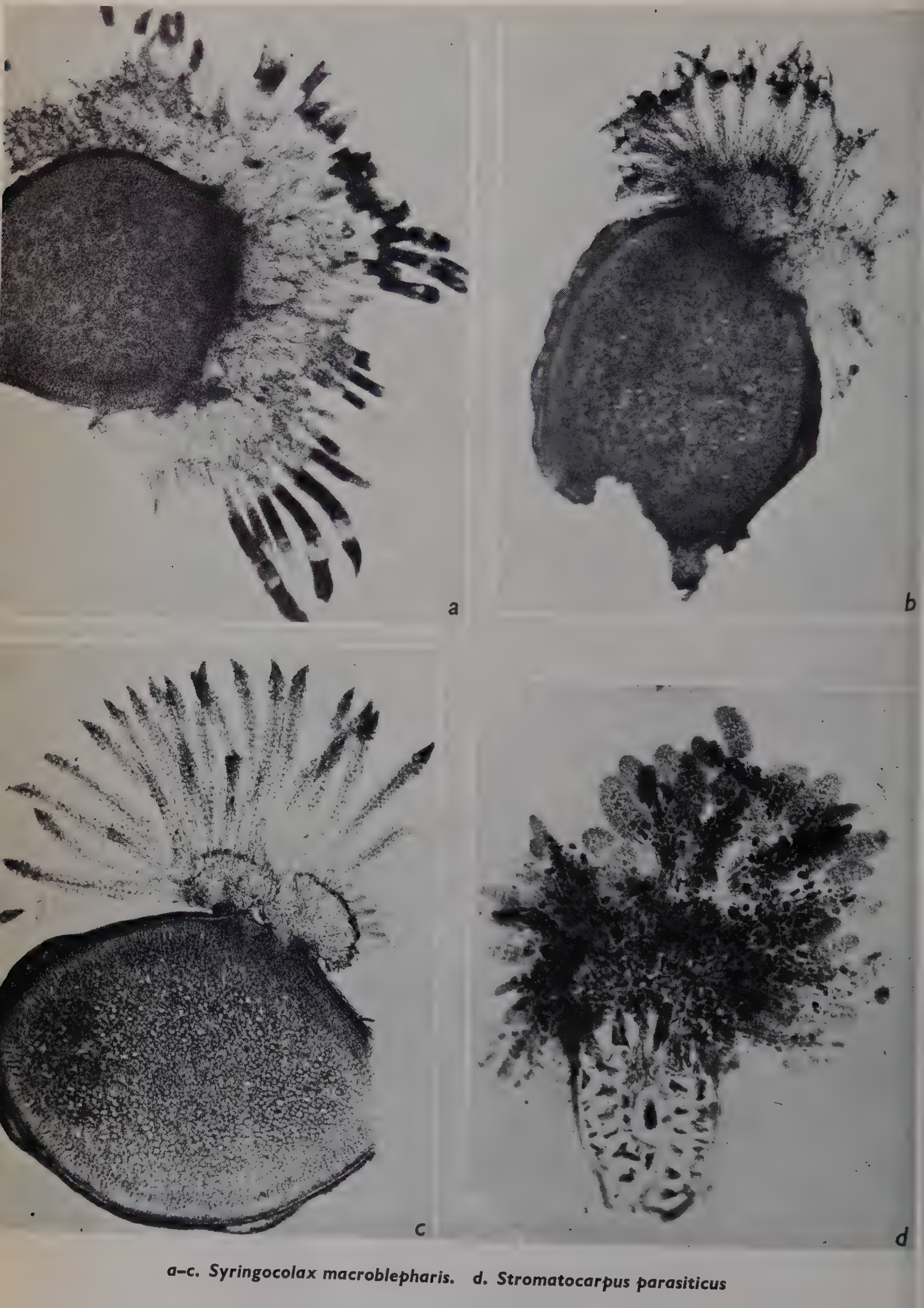
a–c, *Syringocolax macroblepharis* on *Gelidium cartilagineum*, vertical section through pustule; *a*, male; *b*, female; *c*, tetrasporic. *d*, vertical section through *Stromatocarpus parasiticus*, male plant on *Tayloriella virgata*. *a–c*, × 30; *d*, × 55.

Plate 12

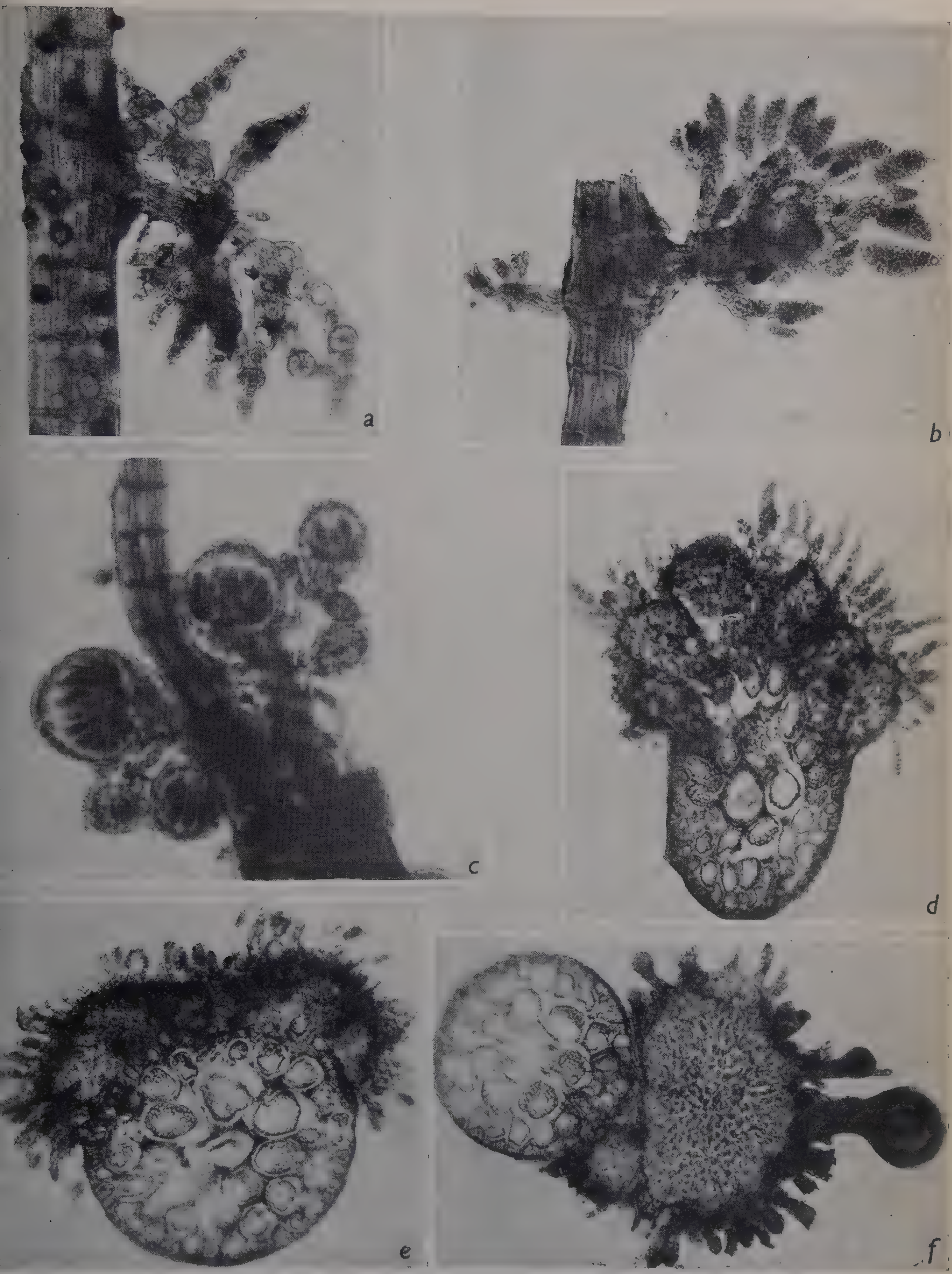
a–c, plants of *Microcolax africana* on *Streblocladia tenuissima*; *a*, tetrasporic; *b*, male; *c*, female, showing ripe cystocarps and carpospores. *d–f*, vertical section through pustules of *Melanocolax velutina* on *Rhodomelopsis africana*; *d*, tetrasporic; *e*, male; *f*, female. *a*, *b*, × 80; *c*, × 60; *d–f*, × 45.



a, b. Choreocolax suhriae. c–e. Choreocolax margaritoides



a–c. Syringocolax macroblepharis. d. Stromatocarpus parasiticus



a–c. Microcolax africana. d–f. Melanocolax velutina

Origin, distribution and phylogenetic affinity of the species of *Mangifera* L.[1]

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(Communicated by Dr P. N. BHADURI, F.L.S.)

(With 3 Maps)

[Read 21 February 1952]

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I. INTRODUCTION

The present paper is based on a series of investigations on the taxonomy, cytology, anatomy, pollen-analysis and geographical distribution of the species of *Mangifera* L. (Mukherjee, 1948*a*, *b*, 1949*a–c*, 1950 *a–c*, 1951*a*, *b*). The chief basis of this work is the taxonomic study from an intensive examination of all the collections of the genus, numbering more than 1000 sheets, accumulated in the various Asiatic Herbaria, e.g. the Royal Botanic Gardens at Calcutta and Singapore; the Forest Herbaria at Dehra Dun, Assam and Burma; the Buitenzorg Herbarium, Java; the Sarawak Museum, Borneo; and the Philippines National Herbarium. The distribution areas of the individual species, which form the main basis of analysis, have been recorded from the herbarium collections and from the various published 'Floras'.

Such an analysis may not represent all the points of distribution within the areas occupied by individual species, as it is well known that Malaysia, containing most of the species, has large areas (of Sumatra, Borneo, Celebes, New Guinea, etc.) still unexplored (Airy Shaw, 1943). But a comparison of the distribution areas of all the species will give some reliable data, available under the present limitations of our knowledge, to formulate a theory as regards their origin.

The results obtained from an analysis of the data of phytogeographical distribution will further be corroborated from other evidences such as paleo-geography, geological history of the area, and cytological observations by the author.

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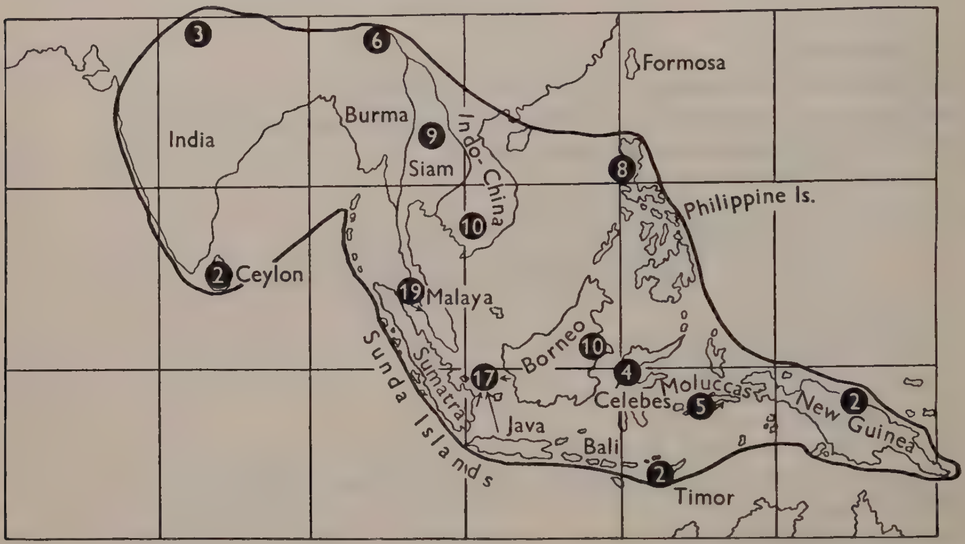
[1] This paper is based on a series of investigations on *Mangifera* L. conducted by the author at the Calcutta University.

II. PRESENT AREA OF DISTRIBUTION OF THE SPECIES AND SECTIONS

The distribution of the forty-one valid species of *Mangifera*, known to occur throughout the world (Mukherjee, 1949*a*), shows that the natural area of the genus is sharp, and delimited by India and Ceylon in the west to the Philippines and New Guinea in the east, the Himalayas, Yunnan (China) and Indo-China in the north to the arc of islands comprising the Sunda and the Sulu Archipelago in the Indian Ocean in the south (Map 1). The occurrence of some species, especially *M. indica* L., outside this area is due to their introduction by human agency in regions far distant from the original home, e.g. in America, Africa, Australia, China, Formosa, etc., due to their economic importance. I would, therefore, feel it safe to delimit the area of distribution to India and Malaysia as outlined above. This conclusion is supported by the geological and geographical factors to be discussed later. This area roughly corresponds with the 'Indian Monsoon Region' and the 'Eastern equatorial Region' proposed by Burkill (1943); and with the 'Indian', 'Continental South-east Asiatic' and 'Malayan Archipelago Regions' of the 'Indo-Malayan subkingdom' within the 'Palaeotropical Kingdom', recently classified by Good (1947).



Map 1. Range of distribution of the genus. The thick black line indicates the limits of distribution and the numbers within circles indicate the number of species occurring in the different countries.

TABLE 1. *Geographical distribution of the species of* Mangifera

India (including Assam, Chittagong and Sikkim)	3	Sumatra	11
Ceylon	2	Java	9
Andaman Islands	3	Borneo	10
Burma	6	Bali	2
Siam	9	Philippines	8
Indo-China	10	Celebes	4
Malay Peninsula	19	Moluccas	5
China	1	Timor	2
		New Guinea	2

Table 1 gives the number of species occurring in the various areas, as delimited by political divisions. For a phytogeographical analysis, various divisions have been suggested by Wallace (1876), Engler (1882), Drude (1887), Clarke (1898) and others. There has naturally been some confusion as regards the categories 'Region', 'Subregion', 'Province', and 'Gebieten' or 'Territories' assigned to these areas. From Burkill's consideration, it appears reasonable to divide the whole zone of distribution of the genus into the following areas:

(1) *India* (including the Himalayas, Assam and Chittagong Hill tracts).
(2) *Ceylon.*
(3) *Andamans.*
(4) *Eastern Peninsula* (including Burma, Siam and Indo-China).
(5) *Malay Peninsula.*
(6) *Sunda Islands* (Sumatra, Java, Borneo and Bali).
(7) *Philippines.*
(8) *Eastern Malaysia* (all the lands east of Wallace's line and west of Weber's line as modified by Lydekker).
(9) *New Guinea.*

The total numbers of species of *Mangifera* in each of the above areas, along with the number of 'endemics' and 'wides', are given in Table 2.

TABLE 2

	Total	Endemic	Wide
India	3	1	2
Ceylon	2	1	1
Andamans	3	1	2
Eastern Peninsula	14	5	9
Malay Peninsula	19	8	11
Sunda Islands	16	6	10
Philippines	8	4	4
Eastern Malaysia	6	2	4
New Guinea	2	—	2

The table shows that the highest number of species and endemics occurs in the Malay Peninsula. The next areas are the Sunda Islands and the Eastern Peninsula. The three main islands of the Sunda Archipelago present almost an equal number of species (viz. Sumatra 11, Borneo 10 and Java 9). In the Eastern Peninsula, Indo-China and Siam possess ten and nine species respectively of which only one is endemic, whereas Burma has only six species with no endemic. The Philippines present interesting features in containing a high percentage of endemics, four out of eight (50 %), although situated at the limits of generic distribution. Several of the widely distributed species are manifestly introduced here, particularly *M. indica* and *M. caesia*. Another striking feature is the paucity of the *Mangifera* species in Eastern Malaysia and New Guinea. Such paucity of the Asiatic species in Eastern Malaysia is well known in the Dipterocarps (Merrill, 1923).

It is evident, from the data presented above, that the Eastern Peninsula along with the Malay Peninsula and the Sunda lands are essentially the regions in which the genus has reached its maximum development as regards the number of species. In consideration of the concentration of species under both the categories 'Total number' and 'Endemics', it is clear that the Malay Peninsula, either alone or along with the Eastern Peninsula, is the centre of origin of the genus. Further verification of this view will be made from other aspects. The above conclusion as regards the centre of origin has been made from the number of species contained in the whole genus. But all the species in a genus being not uniform in character are not of equal value. Hence Szymkiewicz (1934, 1936, 1937) suggested that analogous calculations be made for each section or subgenus. Cain (1944) has remarked that 'in general it is apparent that Szymkiewicz's method of handling generic statistics for the indication of centers is one that provides more significant data than the old method of merely listing species numbers'. Separate analysis of the two sections of *Mangifera* is therefore given in Table 3. Section I, which has well-developed disk, possesses thirty-four species; whereas Section II, with disk reduced to a pedical or obsolete, has only seven species.

TABLE 3

	Section I			Section II		
Areas	Total	Endemic	Wide	Total	Endemic	Wide
India	3	1	2	—	—	—
Ceylon	2	1	1	—	—	—
Andamans	3	1	2	—	—	—
Eastern Peninsula	10	5	5	4	—	4
Malay Peninsula	12	7	5	7	1	6
Sunda Islands	10	6	4	6	—	6
Eastern Malaysia	4	2	2	2	—	2
Philippines	6	4	2	2	—	2
New Guinea	2	—	2	—	—	—

The data corroborate the findings of Table 2, and show that the areas with maximum concentration of the species are the Eastern Peninsula and the Malay Peninsula, even when the two sections are analysed separately. The remarkable feature in Table 3 is the absence of species belonging to Section II from India, Ceylon, the Andamans and New Guinea.

An examination of the distribution area of the individual species (cf. Mukherjee, 1949*a*) shows that a large number of endemics is present in the genus. Out of a total of forty-one species, twenty-eight are endemics; twenty-two occurring in only one country, five in two countries, and only one in three countries which constitute a botanical area (vide Maps 2 and 3). Among the thirty-four species of Section I, twenty-seven are endemics leaving the remaining seven as wides; whereas six among the seven species of Section II are wides. Although the total number of species under Section II is much less than in Section I, the percentage of 'wides' is higher in the former.

The distribution of *M. pentandra* is of paleo-endemic nature as indicated by its fossil history. *M. duperreana*, *M. cochinchinensis*, *M. lanceolata* and *M. superba* appear to have a similar history, although no fossil evidence is available. But the majority of the remaining species appear to be 'Neo-endemics', especially the local endemics—*M. philippinensis*, *M. merrillii*, *M. siamensis*, *M. zeylanica*, *M. khasiana*, *M. beccarii*, *M. rumphii*, *M. havilandii*, *M. rigida*, *M. longipetiolata*, *M. spathulaefolia*, etc.—restricted to a very small area or one locality only.

III. PAST AREA OF DISTRIBUTION OF *MANGIFERA* DETERMINED FROM THEIR FOSSIL HISTORY

Whatever meagre fossil records are available suggest that the *Anacardiaceae* were developed and widely distributed in both the old and the new world in the Tertiary period, arising perhaps in the early Tertiary or late Cretaceous. In support of this view may be cited the fossil records of *Rhus* and *Pistacia* from Tertiary and Upper Cretaceous (Bews, 1927); *Anaphrenium* and *Mangifera* from Eocene of Germany; *Dracontomelum*, *Xylocarya* and *Odina* from Eocene of England; *Spondias* from Eocene of England and Pliocene of Brazil; and *Metopium* from Eocene of Texas, Mississippi and Tennessee in America (Darrah, 1939).

Seward (1912) described three fossils of *Anacardiaceae* from leaf impressions, contained in a block of shale from Margherita, Assam, and identified them as *Buchanania latifolia*, *Semecarpus anacardium*, and *Mangifera pentandra*. He doubtfully suggested that the fossils belonged to the Tertiary rather than to the Cretaceous period as the evidences were not sufficiently convincing.

The above records suggest that *Mangifera* was present in the Eocene period, and perhaps in the Cretaceous also. But its occurrence in Germany appears to be doubtful, though not improbable in view of the retrogressive nature of distribution of many tropical plants, e.g. *Nipa* and *Sabal* palms, etc.

The fossil record of *M. pentrandra* from Assam suggests that its distribution is retrogressive, as it is restricted at present to certain localities of Malaya only, where it grows better than the common mango. We may accept this as a paleo-endemic species, as it is phylogenetically older, due to the presence of five fully developed stamens.

IV. CAUSES FOR DISTRIBUTION IN THE PRESENT AREA

(*a*) *Geological history*

The geological history of Malaysia has been extensively discussed by Molengraaff (1921), Merrill (1923), Du Toit (1937) and in a Symposium on the subject at the Linnean Society, London (1943). The consensus of opinion is that there were two definite continental platforms in the Asiatic-Australian region, now delimited by the Asiatic and Australian continental shelves, and since the early Tertiary these had been separated by an area (extending from Lombok and Celebes to New Guinea), which was constantly in an archipelagic condition. The Asiatic or the Sunda shelf carried upon it all the Sunda islands, Sumatra, Java, Borneo, and the intervening smaller islands; the Australian or the Sahul shelf carried the island of New Guinea. In the Pleistocene, and probably in the immediately preceding epoch Sumatra, Borneo, Java, and the islands eastward of Java to and including Bali, as well as the Balabac-Palawan-Calamian group in the Philippines and probably the Sulu Archipelago, were connected at times with the Asiatic continent via Borneo, and New Guinea was connected with Australia; but there was no direct connexion across the narrow Macassar Strait between Celebes and Borneo.

In the Philippines, the earliest geological formations are from the Jurassic. There were occasional connexions between various groups of islands, and the sea was very shallow between them in the Pliocene (Merrill, 1923).

(*b*) *Climatology—past and present*

'Geologists are in agreement that the Cretaceous was a period of remarkable climatic uniformity, in which the strictly tropical types of vegetation extended far to the north and to the south' (Merrill, 1926). Since that period there has been strongly differentiated climatic zonation due to climatic fluctuation in most parts of the earth (Airy Shaw, 1943). But there has been practically no change during this period in the general climatic conditions in the equatorial region of Malaysia, except at the high altitude areas. Comparative studies of the present flora of Malaysia with the fossil remains by various workers (Schuster, 1911; Irmscher, 1922, 1929; Kubart, 1929; Kräusel, 1929; Kryshtofovich, 1929; Wulff, 1943, etc.) indicate that the low altitude Pleistocene Malaysian flora was practically identical with the present one.

The prominent aspects of the present climate are discussed below. The equatorial regions of Malaysia, lying between 50° N. and S. latitude, are 'characterized by heavy rainfall, great humidity and steady high temperature'. Both to the north and to the south of this belt there are fairly well-marked seasonal variations in the climate. The climate and ecology agree in indicating (1) an extensive region in the equatorial belt, where 29·8–29·9 in. isobars remain constant throughout the year, characterized by tropical rain forest; and (2) a much smaller area, influenced by the 'continentality' of the Australian land-mass, characterized by the presence of mixed deciduous 'monsoon' forest. This latter area comprises the lesser Sunda islands, south-western Celebes, and some parts of Eastern Malaysia, which have a pronounced dry season; some areas having less than twenty rainy days in the driest four months of the year (Airy Shaw, 1943).

(*c*) *Factors affecting distribution of the species*

(i) *Dispersal mechanism*

Plants are distributed as a result of the transport of their seeds by natural agencies only slowly and gradually, gaining new territory step by step, except where they are dispersed by wind. The ecological conditions of new areas should be favourable for spread of the species, and the competition of the existing species should also not be very severe.

The fruits of all the species of *Mangifera* are fleshy drupes of large size, in some quite enormous, much too heavy for wind dispersal, and are not adapted to transport by water. They are therefore carried about mainly by animals, such as monkeys and fruit bats (Ridley, 1930); otherwise they drop on the ground beneath the trees, wherefrom they may later be carried some distance especially on slopes.

The seeds have usually a short period of viability, about a month in the case of *M. indica*. They do not generally withstand drying, which is one of the reasons for their occurrence by the sides of rivers and small nullahs in the shaded forest areas. The trees and the seedlings are adapted to the shade, temperature, moisture, and light conditions characteristic of the tropical evergreen and semi-evergreen forests of India and Malaysia.

Hence, in consideration of the habitat complex of the species of *Mangifera*, their seed and seedling characters, especially the short period of viability, it is necessary to postulate previous land connexion from the Asiatic continent to the Philippines through the Sunda Islands and Borneo at some time in geological history when it was possible for certain species to march unimpeded, in order to explain the present distribution of the species.

(ii) *Influence of man in the distribution of Mangifera spp.*

As some of the species, e.g. *M. indica*, *M. caesia*, *M. foetida*, *M. odorata* and *M. kemanga*, bear good edible fruits, human agency had an important role in their distribution to different regions from their original home. How far the distribution of other species had been effected by man cannot be definitely said.

The history of *M. indica* (the most important fruit species) is briefly discussed below. The occurrence of the multitude of varieties and also wild types throughout India, the distribution of the related species, the presence of an ancient Sanskrit name, and reference in early Sanskrit literature indicate that the mango (*M. indica*) was known to the people of India for a long time and had an origin in the Assam-Burma zone (Mukherjee, 1951 *b*).

The wider dissemination of mango (*M. indica*) started throughout the world with the beginning of commerce between Asia and Europe, as in the case of many other tropical fruits and spices. It is most likely that early in the sixteenth century the Portuguese carried the plants or seeds from Goa to East Africa, and thence to West Africa and adjacent island possessions and subsequently to Brazil.

Whereas the introduction of the mango (*M. indica*) in the Western hemisphere has been through the agency of the Portuguese and the Spanish, its introduction into Malaya and the adjoining islands and other countries of East Asia is very likely due to Indian monks making voyages to those areas during the Buddhist period (fourth and fifth century B.C.) for cultural and religious missions (Mukherjee, 1948 *b*; 1949 *c*).

M. indica is now well-established in various countries of both the hemispheres through the agency of man. Similarly, some species of Section II, e.g. *M. foetida*, *M. odorata*, *M. caesia* and *M. kemanga*, appear to have been introduced to the Philippines and the islands of Eastern and Western Malaysia through human agency as the common mango (*M. indica*) does not grow well in these regions.

(*d*) *Role of isolation on the origin of Mangifera spp.*

It is an established fact that isolation is the essential factor in bringing about taxonomic divergence and in preservation of distinctive genetic constellations delimiting the species. 'In fact, we may define species as the minimum permanently isolated groups'

(Darlington, 1940). The isolating mechanisms may be extrinsic or geographical, as well as intrinsic, i.e. genetic, ecological, or physiological.

In *Mangifera*, a majority of the species (twenty-eight out of forty-one) is endemic and restricted to small areas, with overlapping and contiguous areas with other species (see Maps 2 and 3). In the case of the species occurring in the archipelagic region of Malaysia, the isolating factor is mainly geographical or geological; and the various species might have originated through splitting of the areas and subsequent adaptation to different conditions. But in the case of the continental species, occurring in Malaya and Eastern Peninsula, the isolating mechanism is likely to be either physiological, genetic, or ecological, viz. the divergence of characters in *M. longipetiolata* and *M. quadrifida* is expressedly due to their occurrence at different altitudes within the same area. In the case of Malayan endemics (e.g. *M. lanceolata*, *M. gracilipes*, *M. microphylla*, *M. griffithii*, *M. maingayi*, etc.) occurring within the range of distribution of other species and having ample opportunities for hybridization, the distinct nature of the species is maintained only through intrinsic isolating mechanism.

Not only in *Mangifera*, but in a large number of Indo-Malayan genera, a number of endemics are found occurring within the range of distribution of the allied species. The divergence of the species and the preservation of these endemics can only be explained as due to the effect of isolating factors. Similarly, the preservation of the majority of the species in *Mangifera* has been possible mainly through the effect of isolating factors after creation of the variants.

V. PHYLOGENETIC TAXONOMY

The mode of development of the species of *Mangifera* and their affinities are discussed below to bring out the phylogenetic trend of evolution in the genus, which combined with the phyto-geographical records will indicate the centre of its origin and the history of dispersal from that centre.

(*a*) *Morphological study* (Mukherjee, 1948*a*, 1949*a*)

The morphological study shows that the range of variation is not very great. All the species are trees, mostly tall and attaining a height up to 100–150 ft. and occurring in the valleys and on hill slopes at low altitude (sea-level to 3000 ft.). They thrive best perhaps in the humid localities of Malaysia and generally occur as scattered individuals inside forests.

They show the following features characteristic of the moist-tropical forest type of vegetations: (1) inconspicuous flowers; (2) resting period of the seeds short; (3) buds generally without any covering of dry bud-scales (the lack of bud-scales is usually correlated with the absence of a resting season); (4) large, simple, entire, leathery leaves.

Bews (1927) suggested that the coriaceous texture of the leaves of many ecologically primitive types of tropical hygrophilous trees is correlated with relative inefficiency in their power of water-conduction through the wood. He therefore considered that the trees of *Anacardiaceae* belonging to the moist tropical forests may be regarded as some of the most primitive forms among Angiosperms.

The main features in the range of character variation in different parts are discussed below:

Leaf. The species of Section II, except *M. macrocarpa* (i.e. *M. lagenifera*, *M. foetida*, *M. odorata*, *M. caesia*, *M. kemanga*, and *M. superba*), have very thick coriaceous leaves, which are also quite large (attaining a length of 36 cm. in *M. superba*). *M. macrocarpa* is strikingly different from others in possessing narrow, linear, thin coriaceous or membranaceous leaves, 25–40 × 2·5–5 cm. in size.

The species of Section I, on the other hand, have mostly thin coriaceous or membranaceous leaves. Among the thirty-four species only eleven, viz. *M. oblongifolia*, *M. sclerophylla*, *M. microphylla*, *M. similis*, *M. havilandii*, *M. rumphii*, *M. rigida*, *M. maingayi*, *M. longipetiolata*, *M. quadrifida* and *M. spathulaefolia*, have thickly coriaceous leaves, but these are generally thinner than those of Section II. There is a great range in variation in the shape of leaves (Mukherjee, 1948*a*).

They are alternate except in *M. caesia* var. *verticillata*, where they exhibit the verticillate arrangement (in whorls of four) characteristic of the allied genus *Bouea*, with whorled leaves. Subverticillate leaves are found also in *M. caesia* and *M. kemanga*.

Inflorescence. The numerous small flowers are borne in elongated panicles. The main variation among the species lies in (1) the type of branching, i.e. with an elongated rachis bearing secondary branches showing a pyramidal shape, or with the main axis suppressed and the branches coming out from the tip of vegetative shoots, forming a fascicle; (2) glabrous or pubescent or tomentose nature of the panicle branches; and (3) the length-variation of the panicles.

Flowers. The flowers are tetracyclic except in *M. duperreana* and *M. lagenifera* where they are pentacyclic, with an additional whorl of staminodes. The pentacyclic arrangement of flowers with two whorls of stamens is found in the allied genus *Anacardium*.

The flowers are regular and pentamerous in fourteen species of Section I and all the seven species of Section II, whereas seventeen species of Section I are tetramerous. An intermediate group, containing the remaining three species of Section I, *M. camptosperma*, *M. gedebe* and *M. microphylla*, is very interesting in having pentamerous as well as tetramerous flowers, the transition being very manifest in *M. gedebe*, where the fifth petal in pentamerous flowers is shorter than the others and may possibly be the vanishing member. Hence it may be assumed that the tetramerous species are reduced forms of the pentamerous species, from which they have possibly originated. Any definite view on this subject will, however, require corroboration from a study of the floral anatomy of the species belonging to the two groups.

Petals. The petals have different types of ridges, which are the swollen bases of nerves with some reserve inclusions. *M. caesia*, *M. kemanga* and *M. superba* of Section II have only one central ridge, whereas in other species the ridge is divided either from the base or above into a number of branches which gradually taper at the extremities. In some species of Section I, however, it is trunk-like and ends in broad tuberculate excrescences, separated from the surface of the petals (Mukherjee, 1948*a*).

Stamens. The stamens vary from ten to five in number. Only *M. duperreana* of Section I and *M. lagenifera* of Section II have ten stamens in two whorls, among which five to six are well-developed with normal anthers, the rest reduced to short filamentous staminodes in the inner whorl. The rest of the species have only one whorl of five to four stamens, among which only two species of Section I (*M. cochinchinensis* and *M. pentandra*) have all the five stamens fertile, i.e. with well-developed two-lobed anthers. *M. lanceolata* has three stamens fertile. The remaining thirty-six species have only one fertile stamen and show all stages in the reduction of stamens, from the four almost equally elongated filaments with sterile knob-like anthers, to the species where the staminodes are completely absent (cf. Mukherjee, 1948*a*). The species can be grouped according to the stages they show in the reduction of the stamens:

(i) *Species with filaments almost of same length as the fertile stamen but with barren knob-like anthers*

Section I *M. oblongifolia*
Section II *M. macrocarpa*, *M. foetida* and *M. odorata*

(ii) *Species with filaments very much reduced and with very short barren knob-like anthers attached or absent*

Section I *M. caloneura*
M. indica
M. longipes
M. sylvatica
M. zeylanica
M. camptosperma
M. gedebe

Section II *M. superba*

(iii) *Species with further reduction in stamens, resulting in absence of any anther and the filaments reduced to short, toothlike projections, attached to the disk-lobes*

Section I
M. minor
M. gracilipes
M. sclerophylla
M. merrillii
M. altissima
M. similis
M. maingayi
M. quadrifida
M. spathulaefolia
M. griffithii
M. philippinensis
M. rigida
M. timorensis
M. monandra
M. andamanica

Section II
M. kemanga
M. caesia

(iv) *Species showing further reduction, resulting in complete absence of staminodes, without any vestiges*

Section I
M. siamensis
M. khasiana
M. microphylla
M. beccarii
M. rumphii
M. havilandii
M. longipetiolata

The above discussion suggests clearly that there is a regular gradation in the process of reduction of the stamens. According to the Besseyan theory of the phylogeny of the flowering plants, 'the presence of numerous stamens indicates a more primitive condition than that of few stamens' (Bessey, 1915). The tendency towards reduction in the stamens among the species of *Mangifera*, therefore, indicates that the species with a higher number of stamens in a pentacyclic flower, viz. *M. duperreana* and *M. lagenifera*, are the most primitive in the genus. The species with all the five stamens developed and fertile, viz. *M. pentandra*, *M. cochinchinensis* and *M. macrocarpa*, are more primitive than those possessing only one fertile stamen.

(*b*) *Cytological study* (Mukherjee, 1950*b*, *c*)

In determining the location of the centre of origin of a genus, the value of cytological data as an additional evidence is being increasingly realized. Consequently, the verification of the results from the morphological findings by means of the cytological data is being stressed by recent workers (Lewitsky & Kuzmina, 1927; Hagerup, 1932; Manton, 1934; Anderson & Sax, 1936; Sokolovskaya, 1938; Strelkova, 1938; Babcock, 1942; Darlington & Ammal, 1945, etc.).

Investigation of the cytogenetics of the species of *Mangifera* has consisted of an analysis of three species, *M. indica*, *M. sylvatica* (occurring in India), and *M. caloneura* (occurring in Burma).

It shows that all the three species and twenty-three horticultural varieties and one wild race of *M. indica* have the same chromosome number, $n=20$ and $2n=40$. During meiosis the chromosomes show a regular pairing into twenty bivalents, and their regular disjunction to the two poles. No multivalent formation or any other peculiarity is seen. The three species and the varieties of *M. indica* differ from one another mainly in the total number of satellites and secondary constrictions in their individual complements. The chromosomes are small in size ($0{\cdot}4$–$2{\cdot}0\ \mu$), and can be morphologically distinguished into eight distinct types, according to their size and the presence or absence of primary or secondary constrictions and satellites.

Although the present investigation suggests a stability in chromosome number in the majority of the species of *Mangifera*, future observations, especially on the phylogenetically older species (*M. duperreana*, *M. pentandra*, *M. lagenifera* and *M. cochinchinensis*), may reveal some species with lower chromosome numbers. But the close range of variation in floral structure in the majority of the species (i.e. the one fertile stamen group) suggests that the same chromosome number is likely to be found in most of them.

The stability in chromosome number is also indicated from the distribution of the species in a tropical region that has never been subjected to great climatic changes. The present analysis suggests that the three species which are morphologically allied have an allopolyploid origin through interspecific hybridization accompanied by chromosome doubling. Further differentiation among the varieties of mango (*M. indica*) has taken place through minute gene mutations. How far this process has been responsible for species formation in the whole genus will be discussed later. Evidence from secondary association and other observations suggests that eight may be the basic number for the genus.

(*c*) *Pollen-analysis* (Mukherjee, 1951 *a*)

Investigation on the pollen morphology of thirteen species shows that all the species have similar tri-colpate grains with pitted exine and three longitudinal furrows containing a germ-pore at the centre of each (Table 4).

TABLE 4

	Species	Range (μ)	Average diameter in majority of the grains (μ)
Section I	*M. pentandra*	20–23	22
	M. laurina	20–39	26
	M. longipes	26–36	30
	M. zeylanica	26–30	30
	M. sclerophylla	32–45	39
	M. quadrifida	32–39	37
	M. altissima	18–26	23
	M. monandra	23–32	26
	M. similis	29–32	32
Section II	*M. lagenifera*	26–39	39
	M. foetida	38–45	39
	M. odorata	25–38	32
	M. caesia	29–36	35

The table shows that the range of variation in size is between 20 and 45 μ, and that the average size of the majority of grains in individual species is between 22 and 39 μ. The species of Section II have grains of bigger size than in Section I, except *M. quadrifida* and *M. sclerophylla*. As the size difference in pollen-grains is generally correlated to polyploidy or aneuploidy in a genus, the presence of similar grains in most of the species suggests that they may have the same chromosome number. Those belonging to Section II and *M. quadrifida* and *M. sclerophylla* may, however, show different numbers. The similarity in morphology and size of the grains further corresponds with the close range of variation in the morphology of the species.

(*d*) *Anatomical evidence* (Mukherjee, 1949 *c*)

It was possible to examine the anatomy of only the main flowering axis of the following eight species, as preserved materials of these could be secured from the Buitenzorg and Singapore Botanic Gardens:

Section I		Section II	
Section I	*M. sylvatica*	Section II	*M. foetida*
	M. caloneura		*M. odorata*
	M. quadrifida		*M. lagenifera*
	M. similis		*M. caesia*

The species under Section II are quite representative, whilst those under Section I are fairly representative, as the first two belong to the pentamerous group, and the last two to the tetramerous group.

The investigation shows that there is no marked or clear-cut difference between the anatomical features of the species belonging to Sections I and II. The main distinctive feature in the genus—the resin-ducts—are present both in the bast and pith in a number of species, whereas in others they are present only in the bast.

The main distinction between the species lies in the nature of the epidermis and the hypodermal cells, the amount of sclerenchymatous tissue around the bundles and in the cortex (e.g. in *M. similis* and *M. sylvatica*), and the number of resin-ducts.

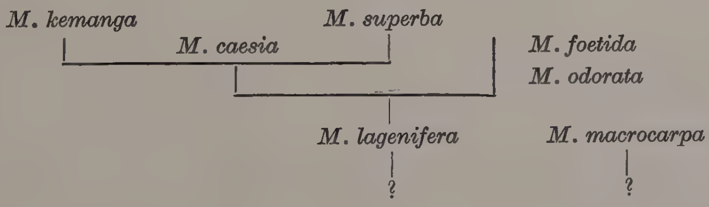
Although no clear-cut distinction may be made between the two sections from the anatomical features, a close correlation in structures between the following pairs of species, viz. *M. sylvatica* and *M. caloneura*, *M. similis* and *M. quadrifida*, *M. foetida* and *M. odorata*, and *M. caesia* and *M. lagenifera*, could nevertheless be observed.

(e) *Conclusions regarding the phylogeny of the species*

From the evidences given above, I shall now discuss the phylogeny of the species in the genus. On the basis of the morphological characters and other evidences, it is possible at least to group the species in their natural alliances and to indicate the phylogenetically older and the more recent species. As regards their actual phylogeny, which may be of linear or reticulate nature, it is rather difficult to indicate from our present knowledge.

Section II has been differentiated early from Section I in the non-development of the disk, and in the presence of large, thickly coriaceous leaves with short petiole, although there is no significant anatomical distinction. The leaves are characteristic of the moist tropical type of trees, which are primitive among the Angiosperms. The floral morphology shows that *M. duperreana* (Section I) and *M. lagenifera* (Section II) possess the most primitive feature in the genus (pentacyclic flowers). Next are the species with all the five stamens fertile, viz. *M. pentandra*, *M. cochinchinensis* (Section I), and *M. macrocarpa* (Section II). The last species is quite distinct from others of Section II in its narrow, linear, coriaceous leaves with large fruits (as large as a child's head).

Among the remaining six species of Section II, *M. lagenifera* is the most primitive as stated before. *M. caesia*, *M. kemanga* and *M. superba* form a closer alliance, each having very thickly coriaceous leaves, and bigger flower with five stamens of which only one is fertile and the rest reduced to short or toothlike filaments, with or without the small knob-like remnant of an anther. *M. foetida* and *M. odorata*, on the other hand, form a separate group due to the presence of less coriaceous leaves, one fertile stamen and four staminodes of shorter unequal filaments with barren knob-like anthers. The above observations indicate the following phylogenetic groupings of species under Section II:



Among the species of Section I, *M. duperreana* is the most primitive due to the presence of pentacyclic flowers and large (13–20 cm. long), thickly coriaceous, rigid leaves characteristic of Section II. Next are *M. pentandra* and *M. cochinchinensis*; the fossil records also indicate that the former is a paleo-endemic species. After these is *M. lanceolata* possessing three fertile stamens and two staminodes. Among the remaining species of Section I, there are three clear groupings; the older being the species with pentamerous flowers, the intermediate having pentamerous as well as tetramerous flowers, and the more recent having tetramerous flowers. *M. oblongifolia* is distinct from others of the pentamerous group in possessing stiff coriaceous, linear-oblong leaves (15–30 × 5–6 cm.), and stamens in the first stage of reduction, i.e. with one fertile stamen and four shorter staminodes with unequal filaments. *M. indica*, *M. sylvatica*, *M. caloneura*, *M. zeylanica*, and *M. longipes* form a close alliance. The first three species possess the same chromosome number and show similarity in their karyotypes and anatomical features. *M. siamensis* and *M. khasiana*, though occurring as endemics in separate areas, show similar features in the reduction of stamens (complete absence of staminodes), and in having fasciculate inflorescences; the former showing more affinity to *M. indica* and the latter to *M. sylvatica*. *M. minor* and *M. gracilipes* have similar staminodes which are short, tooth-like projections without any remnant of anthers. The latter species is very restricted in distribution, being known only from the collections of Maingay, and shows some similarity to *M. sclerophylla* in leaves.

In the intermediate group, *M. camptosperma* is closely allied to *M. caloneura* in the compressed, biscuit-like drupes. *M. gedebe* shows affinity with *M. similis*, and *M. microphylla* with *M. griffithii* and *M. sclerophylla*.

The seventeen species of Section I, possessing tetramerous flowers, can be grouped primarily into two divergent branches on the presence of thick coriaceous, sclerophyllous leaves, or of thinner coriaceous or membranaceous leaves. To the first group belong the following species, among which the first is distinct from others:

M. sclerophylla
M. similis
M. havilandi
M. rigida
M. maingayi
M. longipetiolata
M. quadrifida
M. spathulaefolia

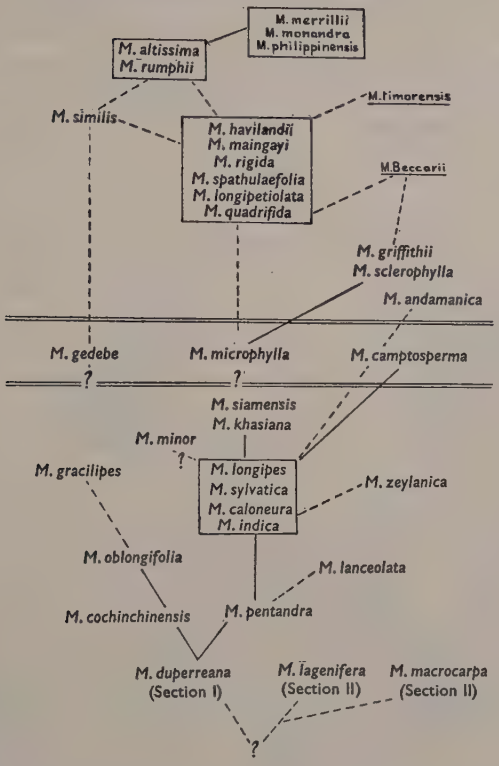
Among the rest, *M. beccarii* shows affinity with *M. griffithii*, whereas *M. merrillii* and *M. philippinensis* are allied to *M. monandra*. *M. altissima* and *M. rumphii* are closely related; the former has some affinity with *M. quadrifida*. *M. timorensis* appears to be distinct.

Thus after a consideration of inter-relationships among the species on the basis of their relatively primitive and more progressive morphological characters, and also of their anatomical, cytological and pollen-characters, the phylogenetic relationship shown on the chart opposite between the various species of *Mangifera* may be postulated, but the actual process by which it has taken place is difficult to state. The progenitors of the different species are hypothetical (especially those marked with a dotted line).

The chart gives some idea about the phylogenetic trend of the species, and their affinities and probable alliances, on the basis of knowledge at present available. It becomes apparent that the range of variation in the genus is limited, and there occur groups of species with almost similar characters having little variation and therefore at the same level of evolution. Cytological study of three species has shown that they have the same chromosome number and similar karyotypes. Pollen analysis has indicated similar shapes and almost similar range of size variation in thirteen species belonging to both the sections. Anatomy of the eight species also does not show much difference. All these evidences suggest the slow, intergrading range of variation in the genus, with the specific characters merging with each other. The cytological study further indicates a stabilized chromosome number in the majority of the species of one fertile stamen group of Section I. Hence it appears that the genus has, at present, a slow rate of evolution, and the major groups of species have become stabilized since their early differentiation.

The distribution area of the species of Sections I and II individually and in groups is given in the accompanying charts (Maps 2 and 3).

PHYLOGENETIC TREND AMONG THE SPECIES OF MANGIFERA (SECTION I)



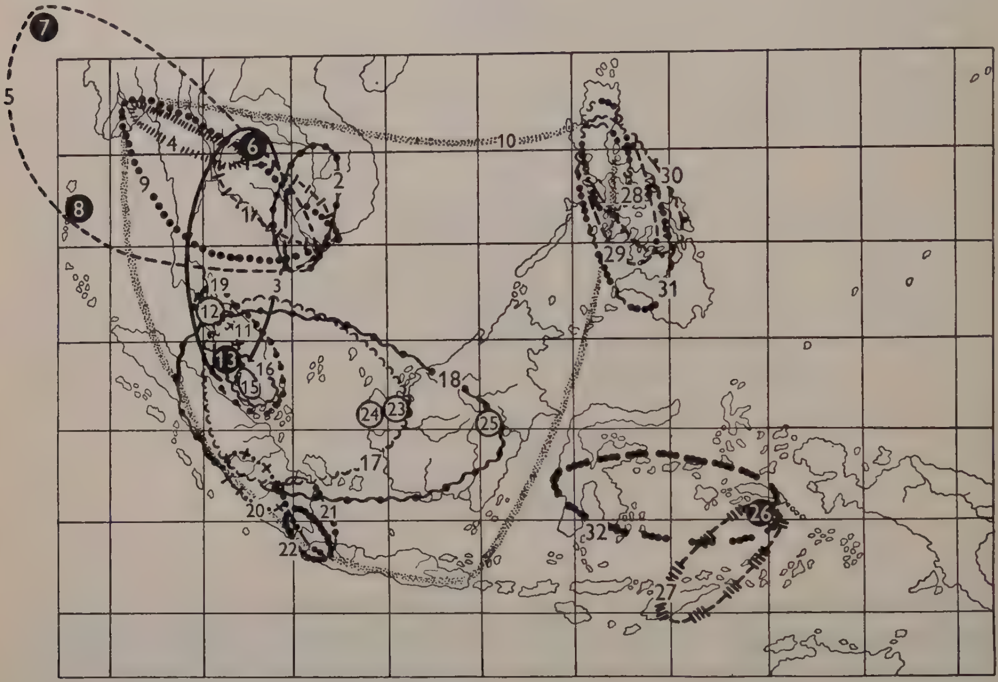
VI. ORIGIN OF THE GENUS AND EVOLUTION OF THE SPECIES AND THEIR MIGRATION

The phyto-geographical study of the genus shows that the largest number of species of both Sections I and II, separately as well as taken together, occur in the Malay Peninsula. The areas next in number of species are the Sunda Islands and the Eastern Peninsula (comprising Burma, Siam and Indo-China). Hence it is in the continental region, covered by Burma, Siam, Indo-China and the Malay Pensinula, that the great majority of the species (about twenty out of forty-one) occur. This is clearly the area where the greatest diversity and wealth of forms in the genus are concentrated. We can take this as the *mass centre* or *centre of maximum variation* in the genus (Turrill, 1939). Although the highest number of species of both the sections are concentrated in the Malay peninsula, the centre of origin of the genus cannot be restricted to that area alone, as both the phylogenetically oldest species (*M. duperreana* and *M. lagenifera*) occur in Siam and Indo-China (Eastern Peninsula), and the former is absent from the Malay Peninsula. Among the species having all the five stamens fertile and unreduced, *M. cochinchinensis* is restricted to Indo-China, and *M. macrocarpa* is present both in Indo-China and Malaya. *M. pentandra*, although at present restricted to the Malay Peninsula, had a former wider range extending to Assam, where fossil leaf-impressions of the species have been discovered. Hence from the morphological, phyto-geographical and fossil evidence it appears that the genus had its origin somewhere in the Burma-Siam-Indo-Chinese area or in the Malayan area.

As the paleobotanical records are very meagre, the actual area which the genus occupied during previous geological ages cannot be ascertained, but the phyto-geographical data give an idea about the present-day concentration of the species, and indicate the centre not of the past but of the present development of the genus. However, the occurrence of the phylogenetically primitive species in Indo-China and Malay

Peninsula suggests their origin in that region, wherefrom the species had their further development.

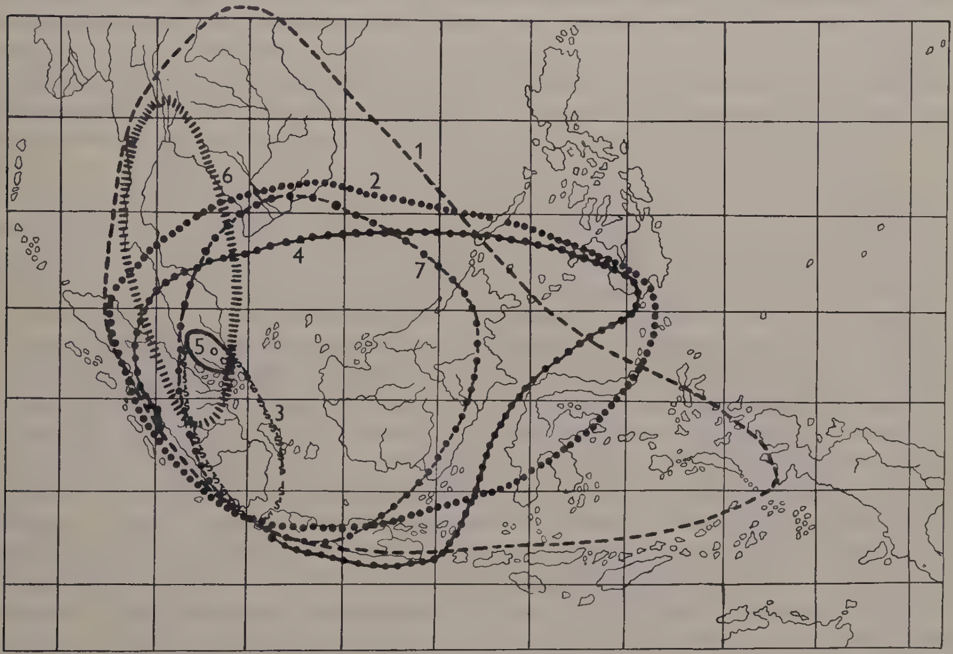
The two main centres are the Assam-Burma-Siam-Indo-Chinese region and the Malay Peninsula (see Maps 2 and 3). The Sunda Islands, the Philippines, and the Celebes-Banda-Timor group form secondary centres of development. The Philippines area is very interesting in view of the fact that among the eight species occurring there, four are endemic.



Map 2. The areas of distribution of the species included in Section I of the genus. The numbers indicate the following species; those within small circles are restricted to one locality only:

1. *M. duperreana*
2. *M. cochinchinensis*
3. *M. oblongifolia*
4. *M. caloneura*
5. *M. sylvatica*
6. *M. siamensis*
7. *M. khasiana*
8. *M. andamanica*
9. *M. camptosperma*
10. *M. longipes*
11. *M. griffithii*
12. *M. lanceolata*
13. *M. gracilipes*
14. *M. longipetiolata*
15. *M. maingayi*
16. *M. microphylla*
17. *M. sclerophylla*
18. *M. quadrifida*
19. *M. pentandra*
20. *M. rigida*
21. *M. similis*
22. *M. gedebe*
23. *M. havilandii*
24. *M. beccarii*
25. *M. spathulaefolia*
26. *M. rumphii*
27. *M. timorensis*
28. *M. altissima*
29. *M. monandra*
30. *M. philippinensis*
31. *M. merrillii*
32. *M. minor*
33. *M. indica* (not included in map)
34. *M. zeylanica* (not included in map)

The most interesting feature of the distribution is the presence of only seven species (four of Section I and three of Section II) in Eastern Malaysia. Among the four species of Section I, only one (*M. indica*) is spread over both the Eastern and the Western Malaysian region, whereas all the three species of Section II occur in both the areas. But *M. indica* is introduced by man in Eastern Malaysia. Out of the six species of Section I, reported from the Philippines, only two are from Western Malaysia; whereas the two species of Section II are present in both the areas. It suggests that the species of Section II had more time to spread from western Malaysia to the Philippines and Eastern Malaysia, in comparison to the species of Section I, only one species of which had spread into the latter area, and that through the agency of man. The species of Section II, therefore, appear to have had a more primitive origin, adapting themselves better to the Equatorial Monsoon Region of Malaysia. The paucity of the species in Eastern Malaysia is attributable to the unstable nature of the area (evident from the geological history), as also to a different type of climate. As the Philippines and the islands of Eastern Malaysia were never connected directly to the Asiatic mainland, except through narrow land-bridges via Borneo and the Sunda Islands, since the Cretaceous when the Angiosperms originated, the species of *Mangifera* with thick fleshy drupes having short viability and unusually slow dispersal mechanism could not find their way into these areas from their seat of origin in the Eastern Peninsula. But the species are more numerous in the Sunda Islands, as they could reach these areas at times when these islands were connected to the Asiatic mainland through the Malay Peninsula.



Map 3. The areas of distribution of the species included in Section II of the genus. The numbers indicate the various species:

1. *M. foetida*	5. *M. superba*
2. *M. odorata*	6. *M. lagenifera*
3. *M. kemanga*	7. *M. macrocarpa*
4. *M. caesia*	

The actual process of species-formation is difficult to postulate, but from a cytogenetic analysis of three species of Section I, it appears that they had an allopolyploid origin. The numerous varieties of *M. indica* and the allied species had subsequently differentiated by gene-mutations and hybridization. Whether these are true gene-mutations or translocation mutants, as in *Datura* (Blakeslee *et al.* 1940), can only be established when the interspecific and intervarietal crosses have been examined. It is rather difficult to indicate the mode of origin of the species of Section II unless some species of that Section are examined cytologically. But the species of Section I except *M. duperreana* (all of which are morphologically very much allied, showing limited range of variation) are indicated to have had similar mode of origin through hybridization and gene-mutations; the distinctive genetic constellation being preserved through isolation. The overlapping and contiguous nature of the areas of distribution of the majority of the species and their occurrence in very scattered isolated groups inside primary tropical forests also suggest that hybridization between different species played a major role in their evolution. This is indicated by the fact that the initial centre of a new hybrid species, especially of *Mangifera* with slow dispersal mechanism, will occupy only a small territory. The initial number of individuals of such a species is determined by the number of seeds produced through hybridization and their successful germination and growth in competition with the vegetation already established in such tropical forests.

The geology and paleogeography of the region indicate that the Eastern Peninsula was a stable region from which the Sunda islands had broken away, whereas Eastern Malaysia was always an unstable area, and the Philippines had a more recent origin. Hence the species of *Mangifera,* the majority of which occur in the Eastern Peninsula, have not passed through any geological revolution since their origin in the Eocene or an earlier period. The climate of this region has also not altered very much or passed through any great change except in the higher mountainous regions during the quaternary glaciation. But the species of *Mangifera* are restricted to the strictly tropical zones at low altitude, extending in the mountains up to 3000 ft., and this altitudinal range has not experienced much change in climate. The unformity in the geological and climatic factors in the region had therefore helped in the stabilization of the characters since the evolution of the genus during the early Tertiary, belonging as it does to one of the more primitive Angiosperm families.

Though the geological and climatic factors are more or less uniform, minor variations in the edaphic and climatic conditions, as well as the inherent tendency for variation within a species, which is a dynamic complex, have helped in the diversification of the forms, leading to the formation of species.

The conclusion derived from an analysis of the above records is that the genus had its origin somewhere in the Eastern or Malay Peninsula, whence two separate lines led to the evolution of the species of Sections I and II; or it might be possible that through *M. duperreana* or *M. cochinchinensis* diversification of the two groups had occurred. The species then spread into India and Ceylon to the west, and to the Philippines through Sunda Islands and Borneo. Very few species reached Eastern Malaysia due to the archipelagic conditions. The origin of the genus possibly took place through allopolyploidy. Mutations have subsequently played an important role in the evolution of the species, the distinctive genetic constellations being maintained mainly through isolation. The main centres of species formation and diversification are the Assam-Burma-Siam-Indo-Chinese area, the Malay Peninsula, the Sunda islands, the Philippines, and the Timor-Moluccas group. In the last-named area the conditions do not appear to be at all favourable for the spread of the genus. The limited range of variation in the morphological, cytological, pollen, and anatomical characters of the species suggests the stabilization of their characters since their origin in the early Tertiary. The diversification and evolution, that is now taking place among the species, is due to the slow mutations and natural hybridization which are always occurring in nature. Selection is ultimately playing its role in the survival of the variants.

VII. SUMMARY

The problem of the origin of the genus *Mangifera* has been discussed in the present paper, with evidence from a thorough analysis of the phytogeographical data and phylogenetic taxonomy of the component species, and also from the climatology (past and present) and geological history of the areas concerned. The phylogenetic taxonomy is based on an exhaustive analysis of the morphological data, with corroborative evidence from cytological, anatomical and pollen morphology studies on the species of the genus, accumulated in the Asiatic herbaria.

The phylogenetic taxonomy indicates that the two groups of species under Sections I and II have differentiated early either from a common ancestor or from some of the

present species (e.g. *M. duperreana* or *M. cochinchinensis*). The species under Section I have undergone further differentiation into mainly three groups: (1) the pentamerous, (2) the tetramerous and (3) the intermediate having both penta- and tetramerous flowers. It appears likely that the second and third groups have evolved from the first group through reduction of floral parts. The stamens have undergone gradual reduction, and series of stages from the presence of five fully developed stamens to those with one developed stamen and complete absence of staminodes are found in the flowers of the various species.

The genus had its origin somewhere in the Eastern Peninsula (comprising Burma-Siam-Indo-China and Malaya), during the Eocene or an earlier period in the Cretaceous. The species have then spread to India and Ceylon in the west, and to Eastern Malaysia and the Philippines through the Sunda Archipelago. The two main centres of species differentiation are the Assam-Burma-Siam-Indo-Chinese region and the Malay Peninsula. Other smaller centres are the Sunda Islands and the Philippines.

The most interesting feature of distribution is the paucity of the species (only seven species out of forty-one) in Eastern Malaysia. Out of the seven species, four belong to Section I and three to Section II. Only one species of Section I is spread over both Eastern and Western Malaysia, but all the three species of Section II are present in both the regions. It, therefore, suggests that the species of Section II had a more primitive origin. They had consequently more time to spread from Western to Eastern Malaysia and to adjust themselves to the Equatorial Monsoon Region of Malaysia. The paucity of the species in Eastern Malaysia is attributable to the unstable archipelagic condition of the region and to the absence of any direct land connexion with the Asiatic mainland since the Cretaceous, when the Angiosperms originated.

The actual process of species-formation is difficult to postulate, but from a cytogenetic analysis of three species of Section I, it is indicated that they had an allopolyploid origin. The numerous varieties of *M. indica* and the two allied species have further differentiated by gene mutations and hybridization. The mode of origin of the species of Section II could not be established as fresh materials for an examination of these species could not be secured from Malaysia during World War II. But the species of Section I, except *M. duperreana*, which are morphologically very much allied, are indicated to have similar mode of origin through hybridization and gene mutations; the distinctive genetic constellation being preserved through isolation. The overlapping and contiguous nature of the areas of distribution of a majority of these species also indicates that hybridization had a major role to play in the process.

The range of variation in the genus is limited, and there occur groups of species with almost similar characters. The limited range of variation in the morphological, cytological, pollen and anatomical structures suggests a stabilization of the characters in the species during the earlier epochs since their origin in the early Tertiary. The diversification and evolution that are now taking place among the species are due to gene-mutations and natural hybridization, which are always occurring in nature. Selection is ultimately playing its role in the survival of the variants.

VIII. Acknowledgement

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Studies in the Bangioideae. 2. The Conchocelis-phase of Porphyra sp. in Pollicipes cornucopia Leach at Roscoff. By Kathleen M. Drew and K. Sylvia Richards

(Communicated by Prof. H. Graham Cannon, F.R.S., F.L.S.)

(With Plate 13)

[Read 5 February 1953]

Introduction

The genus *Conchocelis*, containing the single species *C. rosea* Batters, was created by Batters for material found in a variety of empty shells, particularly those of *Mya truncata* and *Solen vagina*, dredged in 6–8 fathoms of water between the islands of Great and Little Cumbrae, off the West Coast of Scotland. Batters found it also in similar shells in the intertidal zone. Since its discovery, this alga has been reported to occur on various shores including those of Norway, Sweden, Denmark, and those bordering the Black Sea, as well as those of the N.E. and N.W. United States of America. In addition to the shells listed already, *Conchocelis rosea* is known to occur in empty shells of *Ostrea* spp., *Nassa*, *Mytilus*, *Patella*, *Balanus*, *Buccinum*, *Littorina* and *Cyprina*, as well as the calcareous tubes of *Spirobis* and *Pomatocerous*. *Lithothamnion laevigata* and calcareous stone also provide a suitable matrix for its growth.

Batters (1892) published a precise and well-illustrated account of this microscopic alga, extensive growths of which are visible to the naked eye as pinkish areas in infected shells. The fine and irregularly branched perforating filaments show varying degrees of septation and cells of every imaginable shape. Here and there among the fine filaments and arising from them, Batters found rows of quadrate cells of considerably greater diameter. These he considered to be sporangia and stated that one non-motile spore is liberated from each of the cells of these fertile cell rows or sporangia. Many years later, Rosenvinge (1931) studied this alga, which he found to be common along the Danish shores, and while confirming Batters's observations, considered it possessed pit-connexions between neighbouring cells and must be classed therefore in the Florideae and not the Bangioideae. Batters, with the prior approval of Bornet, had suggested that *Conchocelis rosea* be classed in the Porphyraceae. In addition, Rosenvinge also figures monospores in the fertile cell rows or sporangia (figs. 617 H and 619 E) and indicates that they escape through lateral openings in the walls. Judging by the figures given, this is also the view held by Jao (1937), but while the mechanism by which a growing filament penetrates a calcareous matrix is conceivable, that by which a spore is discharged laterally from a sporangium embedded in such a matrix is not.

Recently, Drew (1949) has demonstrated that when spores of *Porphyra umbilicalis* (L.) Kütz. germinate on sterile shells, they put out germ tubes which penetrate the shells and give rise to growths identical with those described by Batters (1892) and Rosenvinge (1931) under the name of *Conchocelis rosea*. It would appear, therefore, that this so-called autonomous species is but a phase in the life history of *Porphyra*. A fuller account of this experimental work is being prepared for publication, together with observations on the *Conchocelis*-phase of *Porphyra umbilicalis* (L.) Kütz.

Meanwhile, the occurrence of the *Conchocelis*-phase of a species of *Porphyra* in living specimens of the barnacle, *Pollicipes cornucopia* Leach at Roscoff, is worthy of separate record. The attention of the senior author was called to this endozooic algal growth by Miss K. Sylvia Richards, who kindly placed her prepared slides at her disposal for examination and who has also prepared the section of this paper dealing with material and methods. The interest of the material from Finistère lies in the following points. It is the first record of the occurrence of this phase of *Porphyra* on the coast of France, a country on the shores of which *Porphyra* is known to occur, and at the same time, it is growing in the calcareous parts of an attached living organism, found in a definite type of habitat, a point of ecological interest in the consideration of the life history of that species of *Porphyra* to which this *Conchocelis*-phase belongs. In addition, observations on the numerous sporangia or fertile cell rows occurring in this material have resulted in the accumulation of some evidence in favour of the theory that the spores are liberated directly into the sea in a manner to be described and not laterally into the calcareous matrix. The method of preparing the sections on which these observations are based has preserved the material in the positions in which it was growing, and this has been of great help in the elucidation of the method of spore discharge.

Material and methods

Pollicipes cornucopia Leach (Pl. **13**, fig. 1) is one of the Lepadidae, or Pedunculate barnacles. The body is divided into two distinct regions, the peduncle and the capitulum. The peduncular region is covered by a thick cuticle in which the bases of the numerous, small, calcareous scales are embedded. The scales themselves are covered by a thin, brown, cuticular layer. The capitulum is easily distinguished by the numerous calcareous plates of various sizes. The single carina, the paired terga and the paired scuta are the largest and most conspicuous of the capitular plates. These plates, like the peduncular scales, are covered by a thin layer of cuticle. This layer is often ruptured in the capitular region but rarely in the peduncular region. Algae occur only in the plates and scales where the protective cuticular layer has been destroyed.

P. cornucopia is attached to rocks by the product of the cement glands situated at the base of the peduncle. This species appears to occur only where wave action is intense, no specimens being found in rock pools or on rocks in bays. The individuals occur chiefly in the horizontal or slightly oblique cracks up which the water surges. Most specimens inhabit the mid-tidal zone and are to be found hanging from the upper surfaces or situated in the depths of crevices. The barnacles may occur singly or in groups of ten to fifteen individuals.

There is little known concerning the growth rate or length of life of *Pollicipes*, but Batham (1945) working with *P. spinosus* Quoy & Gaimard (a New Zealand species, ecologically similar to the species here considered) provides data showing that a period of five years is necessary for the animal to reach sexual maturity, a further five years to attain full size and probably another five years elapses before death occurs. All specimens of *P. cornucopia* from Roscoff that have been sectioned have been sexually mature.

Specimens of *P. cornucopia*, preserved in 70 % alcohol, were obtained from the marine laboratory at Roscoff, Finistère, in September 1950, and fresh material was collected from an isolated group of rocks, west of Roscoff, in September 1951. These specimens were fixed in Duboscq-Brazil (alcoholic Bouin), Bouin, 10 % formol and Witmarck's Fluid.

All specimens were decalcified in Diaphanol for 5 days and washed in absolute alcohol for 1–2 days. They were cleared in cedarwood oil and embedded in wax of melting-point 54° and sectioned at 10 μ. The sections were stained in Delafields's haematoxylin and eosin and Mallory's triple stain. Most of this work was done on the material obtained in 1950.

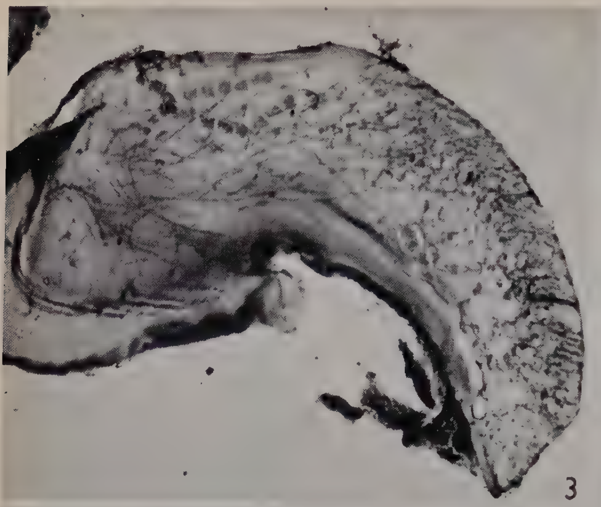
Observations on the *Conchocelis* growths in the scales of *Pollicipes cornucopia*

The infection of *P. cornucopia* by the *Conchocelis* appears to be confined almost exclusively to the peduncular scales, although limited infections have been seen on one of the scuta and a lateral plate of one specimen (Pl. **13**, fig. 1). The scales examined show dense growths of *Conchocelis*, suggesting that the infection is one of long standing. Other algae occur on the outside of the scales, and at least one other unidentified alga is present in a few of the scales. Pl. **13**, fig. 2, shows a longitudinal section of a portion of a peduncle with the fringe of small hooked scales, and one of these scales is shown at a greater magnification in Pl. **13**, fig. 3. The *Conchocelis* is identical with that grown experimentally from spores of *Porphyra umbilicalis* (L.) Kütz, and also with that described by Batters (1892) and Rosenvinge (1931), and so this account is limited to the particular features brought out by this material.

In all the infected scales, the *Conchocelis* shows a definite zonation, the growth being much denser towards the outside of the scale where the filaments are often packed very closely together. The filaments in this position in the scale are much more tortuous than those in the inner and basal portions of the scale, where the majority of the filaments are straight (Pl. **13**, fig. 3). The cells of the filaments immediately beneath the surface are comparatively short and contorted, and form what might be described as a cortical layer. They are 3–4 μ in diameter, but the cells of the straight filaments in the inner layers are around 2 μ in diameter. The staining methods employed have resulted in dense coloration of the tranverse walls in particular. In places, the longitudinal walls appear folded as though there had been some contraction, but it is not known whether this occurred before or during fixation. Fertile cell rows or sporangia are frequent in this material and usually occur in the outer part of the scales. They are irregularly branched and consist of more or less quadrate cells (Pl. **13**, figs. 3, 4) usually 12–13 μ in diameter but ranging from 10 to 20 μ. The method of fixation and preparation of the sections has not been ideal for the preservation of the details of the cell contents, but some of these cells show indications of a stellate plastid (Pl. **13**, fig. 4). In larger and so presumably older sporangia the cell contents are not in close contact with the cell walls especially the transverse walls, and in still others the contents are more or less rounded up and appear to be spores. At such a stage there usually remains little of the transverse walls of the fertile cell rows (Pl. **13**, fig. 5). This is in agreement with two of Rosenvinge's figures (1931) (figs. 617 H and 619 E). In a few instances, the position of the rounded cell contents or spores suggests that after the disappearance of the transverse walls, the spores move along the tubes which are thus formed. Amoeboid movement, a known characteristic of spores of the Bangioideae, may possibly aid their passage along these tubes to the surface of the scale, where they would be liberated into the sea. Many of the fertile cell rows reach the surface of the scales, whilst others appear to be buried deeply. In reality, the latter are portions only of very branched fertile cell rows, which happen to be isolated in that particular section. Some of the scales examined are riddled with empty tubes of the same diameter as the fertile cell rows.

Rosenvinge (1931) and Jao (1937) appear to have considered the escape of the spores through lateral openings in the walls of the fertile cell rows to be possible and figure pores. It is difficult to see how spores could escape in such a manner from sporangia tightly embedded in a calcareous matrix, and should they do so it is reasonable to assume that spores would germinate into *Conchocelis* again. While it has been established that *Conchocelis* growths arise from spores of *Porphyra umbilicalis*, it is still unknown whether the spores from the *Conchocelis* develop directly into the leafy *Porphyra* thalli. Should the latter be the case, liberation of the spores of the *Conchocelis*-phase into the sea and not into the shell inhabited by the *Conchocelis* is more likely.

The density of the growth and the numbers of empty fertile cell rows in some peduncular scales suggest that the *Conchocelis*-phase of *Porphyra* may perennate there for several seasons. As pointed out, it is likely that these barnacles live for several years, and while infection is not likely to take place during their early years when the cuticle of the scales is intact, once the infection is established it appears to persist. As it inhabits the calcareous parts of the barnacle, the death of the animal does not mean the decay of these parts but only a dispersal of them. A more suitable habitat to ensure persistence and dispersal is difficult to conceive. By contrast, the leafy thallus phase of the *Porphyra* being exposed to conditions in the inter-tidal zone is much more subject to seasonal changes than the shell-inhabiting phase even when this occurs in the intertidal zone also. Thus this latter phase provides a perpetual reserve from which the leafy thalli probably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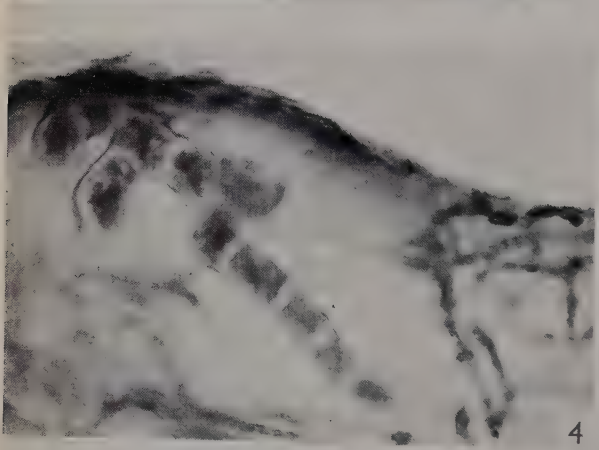
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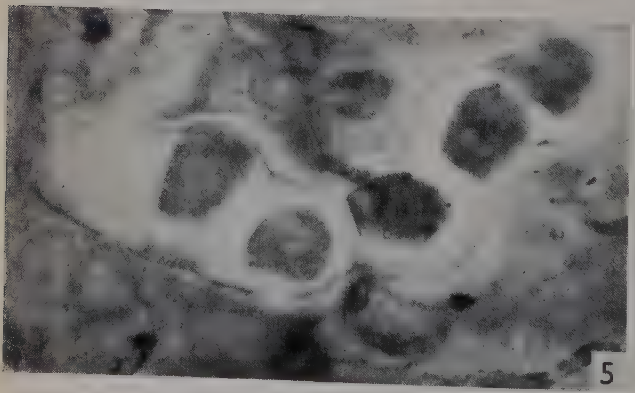
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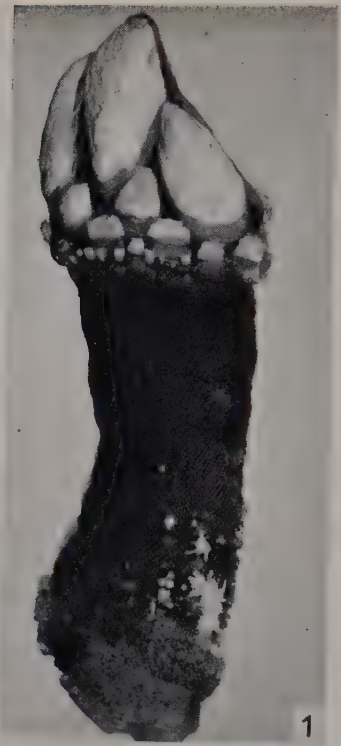
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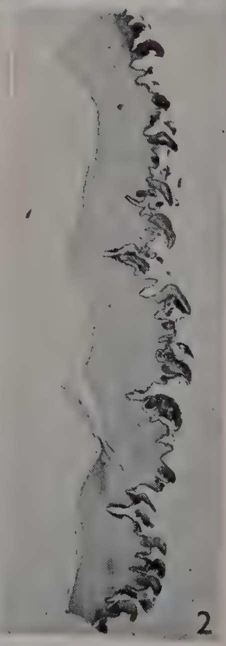
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arise and accounts for the abundance of those species which are found at all times of the year. Those species of *Porphyra*, e.g. *P. linearis* Greville, which are to be found in the form of leafy thalli for only a few months of the year, probably exist at other times as the *Conchocelis*-phase.

These growths of *Conchocelis* in *Pollicipes cornucopia* are indistinguishable from those derived from *Porphyra umbilicalis*. Culture of the *Conchocelis*-phase of various species of *Porphyra* will show how different these phases are morphologically. It may well be that such experiments will show that specific differences are less great than when the same species is grown in different calcareous matrices. Should this be so, it would be impossible to assign a growth of *Conchocelis* to a particular species of *Porphyra* on morphological characters only. It would therefore appear to be premature to ascribe this growth of *Conchocelis* in the peduncular scales of *Pollicipes cornucopia* to a particular species of *Porphyra*.

SUMMARY

The occurrence of the *Conchocelis*-phase of a species of *Porphyra* in the peduncular scales of the barnacle, *Pollicipes cornucopia* at Roscoff, France, is recorded.

This *Conchocelis*-growth closely resembles that described by Batters as *C. rosea*, the only species in the genus created by him. It is also identical with growths of *Conchocelis* originating from spores of *Porphyra umbilicalis* (L.) Kütz. in culture.

A study of the fertile cell rows occurring in the peduncular scales of *P. cornucopia* suggests that, by the breakdown of the transverse walls, tubes are formed and that the spores pass along these to the surface of the scales and are there liberated into the sea.

The ecological importance of the *Conchocelis*-phase in the life history of *Porphyra* is stressed.

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Our thanks are due to Mr E. Ashby for the photographs.

POSTSCRIPT

Since writing the above, spores of *Bangia fuscopurpurea* (Dillw.) Lyngb. from Naples have been germinated, and it has been ascertained that a *Conchocelis*-phase develops from those which give rise to creeping filaments on germination. In the sterile condition, this *Conchocelis*-phase is indistinguishable from the corresponding phase of *Porphyra umbilicalis*, and it remains to be seen whether differences between the sporangia would enable naturally occurring material to be identified.

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EXPLANATION OF PLATE 13

Fig. 1. Specimen of *Pollicipes cornucopia*. ×1.

Fig. 2. Longitudinal section of portion of peduncle, showing scales in section. ×7.

Fig. 3. Longitudinal section of scale showing distribution of *Conchocelis* and both contorted and straight filaments. Note portion of fertile cell-row, composed of large quadrate cells. ×150.

Fig. 4. Fertile cell row at greater magnification. Note indication of stellate plastid. ×500.

Fig. 5. Fertile cell row in which the transverse walls have broken down and the cell contents are rounded up as spores. ×1000.

A contribution to our knowledge of Mallomonas. By KATHARINE HARRIS, B.Sc., University of Reading

(Communicated by Prof. TOM HARRIS, F.R.S., F.L.S.)

(With 90 Text-figures)

[Read 5 February 1953]

ABSTRACT

This paper gives general observations on four species of *Mallomonas*. The chromatophore is single in all, but deeply divided into two lobes. The bristles are always hinged and readily movable. The following new features are described: in *M. leboimii*, the cyst; in *M. lychenensis*, the shredding of the scales and growth of small individuals; in *M. teilingii*, the stages leading to cyst development and in *M. intermedia* var. *gesticulans* var. nov. the structure of the scale and various growth and reproductive stages.

Two internal parasites, ? Protozoa, are described, one on *M. teilingii* and one on *M. intermedia* var. *gesticulans*. These are of importance in destroying a population and in forming cysts which have been mistaken for *Mallomonas* cysts, one forming the basis of a new species of *Mallomonas*.

INTRODUCTION

I have studied the genus of *Mallomonas* of the Chrysomonadales for several years, largely from the systematic point of view. During this time I have made the general observations which are described in this paper.

Samples were collected daily or at longer intervals, in ordinary glass bottles; it was found that most species could live in such bottles for several days provided they were kept away from bright light. As a rule the water was centrifuged before examination, and this seemed to have no ill effect on the *Mallomonas*.

In order to study the scales, cells were dried on the slide and examined both dry and mounted in a medium of high refractive index. I found piperine + antimony tribromide the most satisfactory mountant. Certain species such as *M. lychenensis*, which do not collapse on drying, were disintegrated with chloral hydrate, in order to separate the scales. For this purpose a minute crystal of chloral hydrate, on the tip of a needle, was added to a nearly dry film containing a living specimen.

When giving measurements in describing a species, I have tried to limit myself to individuals which I consider mature. However, I know no way of distinguishing mature from nearly mature individuals, so the lower limit of dimensions is liable to be somewhat arbitrary.

GENERAL NOTES ON SELECTED SPECIES

Mallomonas teilingii Conrad (Conrad, 1933, pp. 45, 63)

My specimens agree closely with the description already given, except that the rear scales are about half the size of the anterior scales and that the chromatophore is single with two lobes (Fig. 1), not double.

Season: November to April, most frequent in February and March. Cysts in February and March.

M. teilingii is fairly common and has been found in twelve different ponds near Reading, occurring in some of them year after year. Most of these ponds are small ones overhung by trees, all occur on agricultural land or by roadsides, some are permanent and some dry up in summer. It has not been found in large lakes or on acid soil. In one closely observed pond it lasted for about 6 weeks, then encysted and disappeared until the following year.

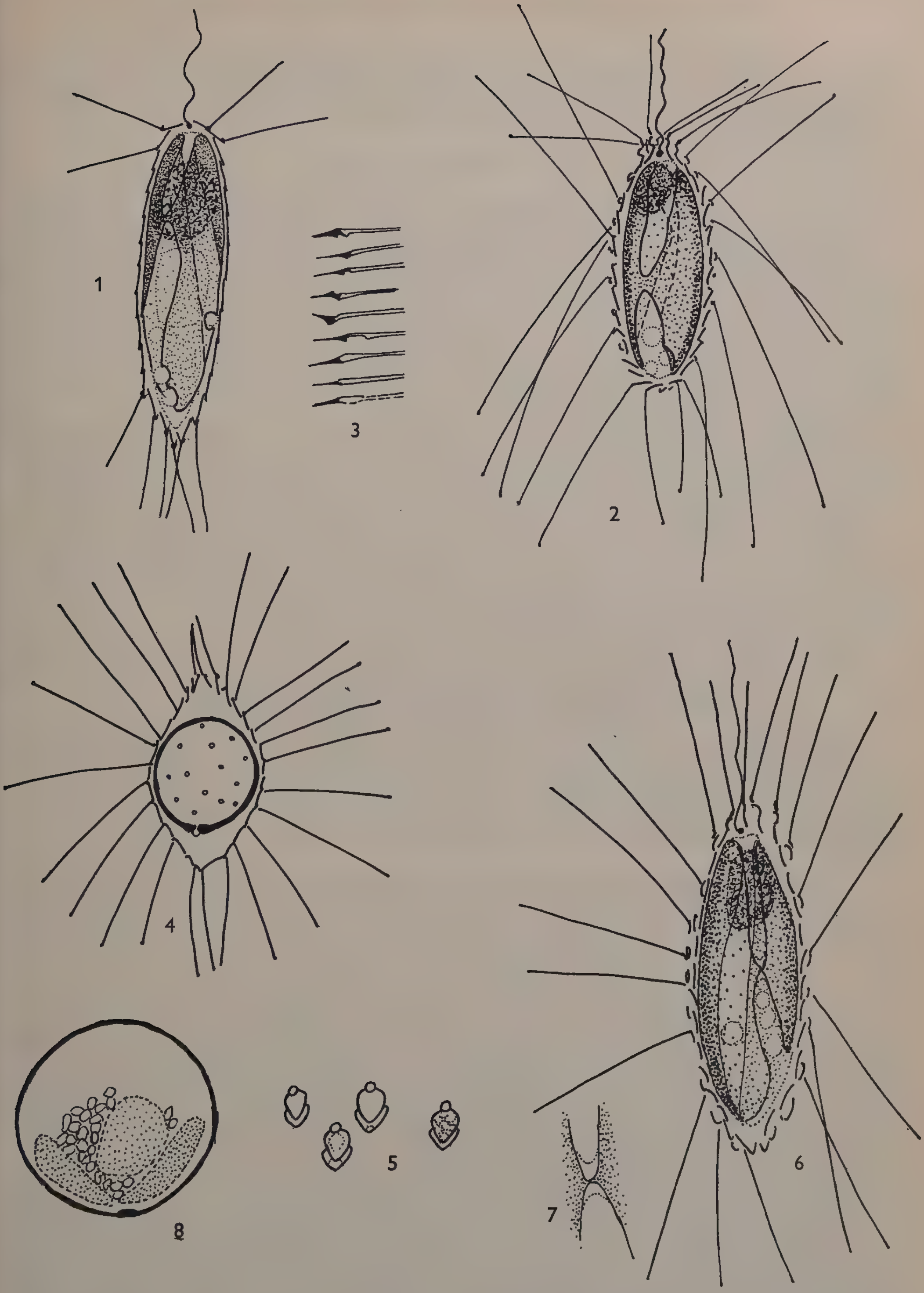


Fig. 1. *M. teilingii*. Figs. 2–5. *M. intermedia* var. *gesticulans*. Fig. 2. Mature cell. Fig. 3. Bristle tips. Fig. 4. Cyst in mother cell. Fig. 5. Scales. Figs. 6–8. *M. leboimii*. Fig. 6. Mature cell, rather small specimen. Fig. 7. Connexion between chromatophore lobes further enlarged. Fig. 8. Cyst. × 1000, except Fig. 7.

Mallomonas intermedia Kisselew var. **gesticulans** var. nov.

Diagnosis. Differt ab *M. intermedia* in apicibus nitentibus setarum angustioribus, acutioribus, et in hypnospora punctata.

Differs from *M. intermedia* in having bristles with narrower, more acute apices, and in the dotted wall of the cyst.

Additional characters: length usually 20–40 μ, rarely larger, scales usually 5–6 μ long by 3·5–4·5 μ wide, cyst 16–17 μ diameter, round, pore small, posterior, rim not prominent.

M. intermedia is incompletely known from Kisselew's (1931) account, but Lund (1942) described specimens, which he identified with it, more fully, and I accept the identification. I presume that Kisselew's figure of the arrangement of the scales is inaccurate, especially as regards the two ends of the cell. The chromatophore, described by Kisselew as single, and by Lund as double, is single and deeply lobed (Fig. 2). The cyst in var. *gesticulans* has a posterior pore (Fig. 4), the position of the pore is not given for the Type by Lund, and has widely spaced not very conspicuous pits.

It should be noted that there are several distinguishable strains of *M. intermedia* in the Reading district besides var. *gesticulans*. They occur in ponds of other types from the ponds which have var. *gesticulans*, and at different seasons, and show minor, but constant, variations from the Type in the scale, bristle tip, in general appearance and in cyst.

Var. *gesticulans* has only been found in five ponds near Reading but reappears annually. All these ponds are small ones on agricultural land and are partly overhung by trees. One of them dries up each summer. In one closely observed pond var. *gesticulans* appeared, swarmed and encysted and disappeared in about a month.

Season: February to June, encysts March to June.

Mallomonas leboimii Bourrelly (see Bourrelly, 1947; and perhaps *M. sphagnicola* Nygaard, 1949)

The identification of my specimens was confirmed by M. Bourrelly. They agree perfectly with Bourrelly's account but I saw a few larger specimens, up to 85 μ long. The cyst (Fig. 8) has not previously been observed; it is smooth, spherical, 28 μ diameter with an inconspicuous posterior pore. The chromatophore is single, deeply divided into two lobes (Figs. 6, 7).

M. leboimii has only been found in two groups of ponds, both containing *Sphagnum*, on acid peaty soils and not overhung by trees. One group of ponds dries up in summer.

Season: December to May, most common February to March, cyst found in February.

Mallomonas lychenensis Conrad (see Conrad, 1938, 1941; Bourrelly, 1947; also var. *tesselata* Nygaard 1949)

The Reading specimens (Figs. 9–16) agree well with those described by Conrad and Bourrelly, but I have noticed a range in the form of the pore of the cyst (Figs. 10–12), which sometimes approaches Nygaard's var. *tesselata*, e.g. Fig. 11. This range is certainly not due to variation in the maturity of the cyst. I believe that there are a number of strains of this species occurring in different ponds.

I am able to add a little to the understanding of the anterior scale, which looks so different when seen in the living cell from when isolated on the slide. Fig. 14 shows an anterior scale which has been slightly damaged, so that the transparent semicircular plate, which usually stands out from the scale (see anterior scales in Fig. 9), is seen lying beside it in the same plane. It appears that this plate is attached at right angles to the scale along one side, and is not easily seen when the scale is lying flat on the slide.

M. lychenensis is very common indeed around Reading, and is found in a large variety of ponds on different soils, but not in large lakes. It has been found in every month of the year except September, but is most commonly seen in February and March. Cysts may be found in every month when the species occurs and may persist in the water for weeks after the motile individuals have disappeared. In one closely observed pond it appeared, swarmed, encysted and disappeared three times between February and July, when the pond dried up. In other ponds I believe it only makes one appearance in the year.

Stages in the life cycle

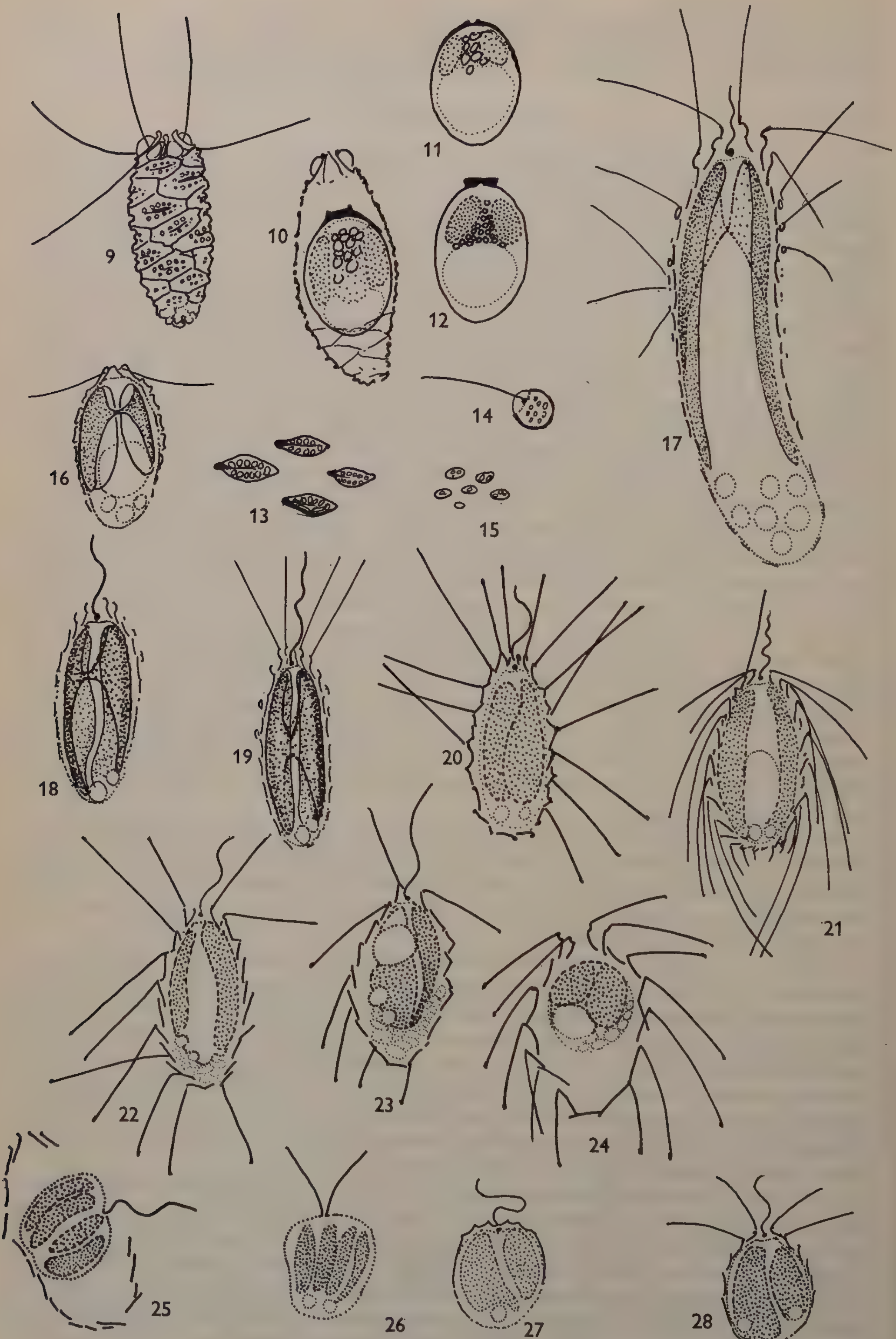
No one seems to have kept *Mallomonas* successfully in culture, though it will often survive, in slowly diminishing numbers, in a bottle of pond water for a week or two, occasionally more, even showing a certain amount of development. My description is based on a series of observations of *M. intermedia* var. *gesticulans* taken from a pond at intervals of a day or two, and is supported by scattered observations of other species. The study reveals such a variation in the size and shape of the cells and the distribution of the bristles that one asks oneself whether there is any possibility of confusion of one or more species. I do not think this is the case. The material was taken from a well-studied pond which had been examined from time to time for years, whose flora was well known and contained no mature individuals, other than those of var. *gesticulans*, to which the young stages could belong. Intermediates were seen between most of the stages, and some of the changes took place so quickly that they could be observed in a single individual on the slide. There is certainly a risk that some of the changes may have been hastened, or brought about, by the bright illumination or other condition of examination, and where this seems likely I have mentioned it in my description.

Stage 1. *Earliest appearance. Mallomonas* must be present in the pond as a cyst before it appears as a flagellate, though I have never been fortunate enough to see the germination of the cyst. It seems likely that, after germination, it is present in the water as an ill-characterized soft-bodied Chrysomonad, for at the beginning of the *Mallomonas* season one may often see such an individual developing scales at its anterior end (Figs. 18, 19). These scales are normal in shape, rather delicate and may have bristles or not. The posterior end of the cell is at first naked, but later produces scattered scales on the surface of the protoplasm. Such forms intergrade with the normal *Mallomonas* (Figs. 18–21). I have seen similar forms in *M. leboimii* (Fig. 17) which, being large, shows this stage particularly well, also in *M. lychenensis* (Fig. 16), and in *M. acaroides* Perty var. *tatrica* Woloszynska (1939), *M. doignonii* Bourrelly (1951), *M. heterospina* Lund (1942), and in two undescribed species.

The *Mallomonas* may be present in the water in the early and mature stages in small numbers, for several weeks. It frequently seems to be intermittent in a particular pond, possibly because it is a small and shifting population. It increases, gradually at first, and later rapidly, to a climax which may be called swarming. The method of increase during this early period is not known.

Stage 2. *Liberation of the protoplast.* This occurs in a medium-sized cell. Numerous contractile vacuoles form at the posterior end of the cell, spreading later to the sides and anterior end. The protoplast seems to move in its shell as large contractile vacuoles form and disappear (Figs. 22, 23). The protoplast then withdraws itself from the ends of the cell and collects in a spherical mass towards the middle (Fig. 24). Such a sphere is then liberated through a break in the armour (Fig. 25) or by the complete break-up of the armour. This process was watched on many occasions and was seen also in *M. lychenensis*. The escaping protoplast was about 12 μ in diameter, with two or four chromatophore lobes, and might have or not have a flagellum.

Sometimes the armour broke up before the protoplast had formed itself into a sphere, and the contents poured out forming an irregular mass of protoplasm surrounded by large contractile vacuoles. On one occasion I watched such a mass round itself off and develop a membrane. It is interesting to compare this with accounts given by Conrad (1914) for *M. mirabilis* and Carter (1937) for *M. anglica* of the liberation of the protoplast in an amoeboid condition. Their figures resemble the appearance of the protoplast as I saw it, but I did not see any pseudopodia, such as Conrad describes. I did not watch the



Figs. 9–28. For legends see p. 93.

protoplasts for more than 20 minutes, nor did I keep them in a hanging drop. Except for these accounts I should have attributed the pouring out of the protoplast from the cell to some abnormal condition, precursor of death, but in the light of that work, and of the single example described above, I am inclined to reserve judgement.

At this time the water was full of many stages of var. *gesticulans*, including naked protoplasts with two or four chromatophore lobes and with or without a flagellum, or rarely with two flagella. There were also protoplasts which showed a few scales at the anterior end, and all stages from this to the round oval *Mallomonas* cell covered with scales (Figs. 26–28). I have no direct evidence that one of these stages developed from another, only the presumptive evidence of intermediate types.

Stage 3. *Longitudinal division.* Longitudinal division has been described by Carter (1937) for *M. anglica.* I saw it in several species, including *M. allorgei* (Deflandre) Conrad, *M. lychenensis*, *M. akrokomos* Ruttner, *M. acaroides* var. *tatrica*, and it usually took 10–15 minutes. The following account is based on *M. intermedia* var. *gesticulans*, and the figures represent a single individual over a period of 10 minutes (Figs. 29–34). As a rule the nucleus and chromatophore divide before the flagellum. In this case only two chromatophore lobes were visible at the beginning, and it is possible either that the other two were obscured from view or that the chromatophore divided later. The scales in the dividing cell looked loose and irregular, and some bristles came off and floated away as I watched. As division proceeded new scales formed on the line of fission so quickly that the protoplasm was never seen without them, and as the daughter cells separated new rear bristles appeared like viscous threads being drawn out. The scales of the daughter cells were regular and closely fitting, but I do not know how they were related to the old ones. No new anterior bristles appeared while I watched.

Stage 4. '*Small Ovals.*' The smallest of these cells was 10 × 7 μ (Figs. 35–37), and all sizes were present between this and ordinary mature cells. Fig. 35 shows what I think is an early condition of this stage, showing scales only at the anterior end and suggesting that it has arisen from a soft-bodied Chrysomonad. The scales of these 'Small Ovals' are similar to the mature scale but smaller and more delicate (Fig. 38), and two chromatophore lobes were present, whether joined or not was not observed. These individuals seem to grow into ordinary mature cells, but it was impossible to tell whether an intermediate cell such as Fig. 39 had developed from a 'Small Oval' or not. 'Small Ovals' occur only at the swarming period of var. *gesticulans* and have not been observed in any other species, possibly because they closely resemble the 'Small Spheres' and may in some species be indistinguishable from them.

Stage 5. '*Small spheres.*' These are spherical motile cells from 8 to 13 μ in diameter with small delicate scales (Figs. 40–42). They are distinguishable from the 'Small Ovals' only in their shape. They may have either two or four chromatophore lobes. The specimens of *M. lychenensis*, shown in Figs. 49, 50, may represent this stage and I have also seen it in *M. acaroides* var. *tatrica*.

I saw one 'Small Sphere' of var. *gesticulans* burst, liberating its contents, which immediately divided into two parts which rounded off forming two non-motile protoplasts (Figs. 43–46). This process was observed many times in *M. acaroides* var. *tatrica*, the two new protoplasts always showing characteristic markings at one end. This process must be regarded with reserve and may be an abnormal one leading to death. Clearly, however, the presence of four chromatophore lobes suggests that division is imminent and

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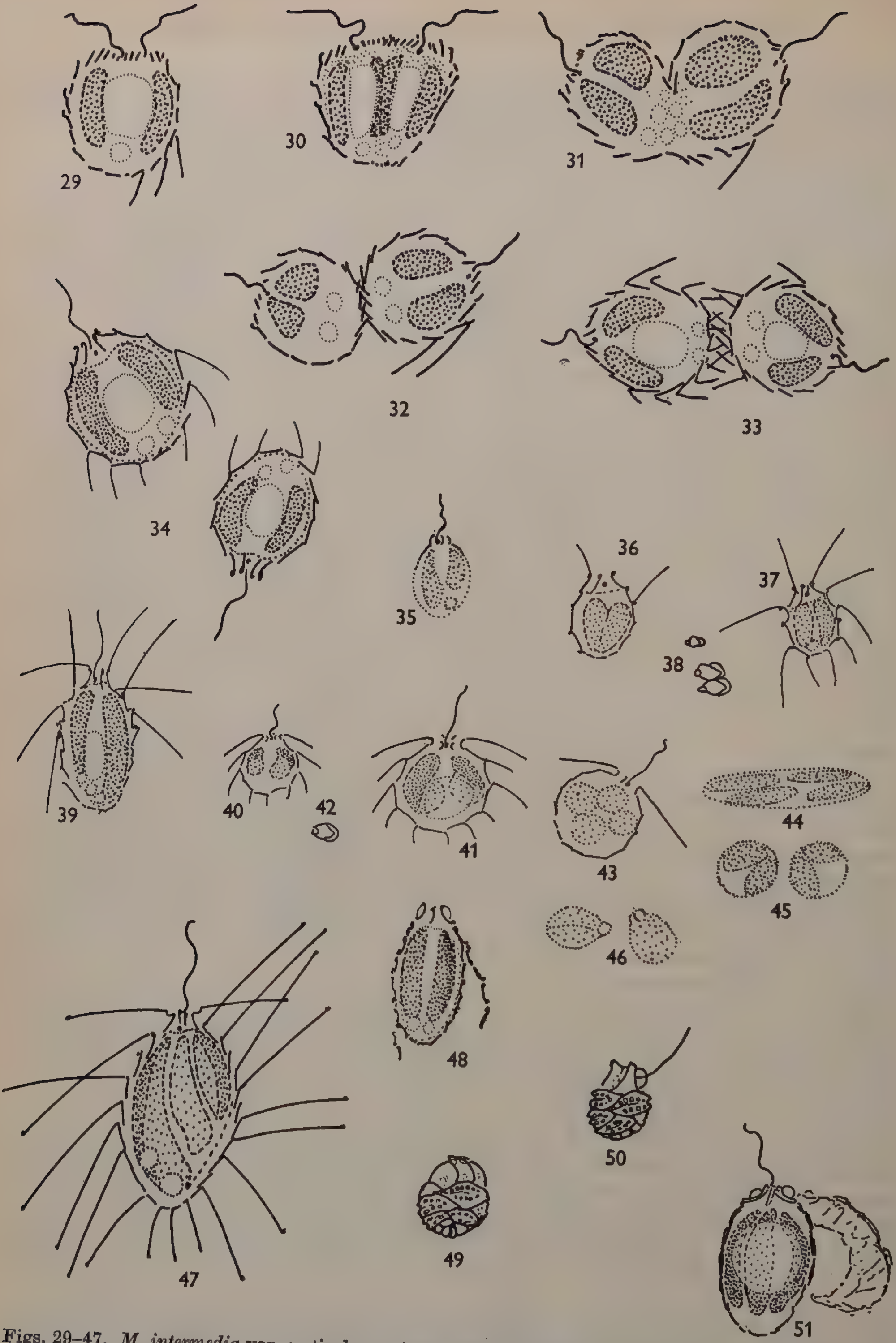
Figs. 9–16. *M. lychenensis*. Fig. 9. Mature cell. Figs. 10–12. Cysts. Fig. 13. Body scales. Fig. 14. Anterior scale damaged so that silica plate is in same plane as scale. Fig. 15. Rear scales. Fig. 16. Immature cell. Fig. 17. *M. leboimii*, immature cell. Figs. 18–28. *M. intermedia* var. *gesticulans*. Figs. 18–21. Immature to nearly mature cells. Figs. 22, 23. Figures from same cell preparing to liberate protoplast. Fig. 24. Spherical protoplast ready for liberation. Fig. 25. Liberation of protoplast. Fig. 26. Naked protoplast with two flagella. Figs. 27, 28. Protoplasts producing scales. × 1000.



Figs. 29–47. *M. intermedia* var. *gesticulans*. Figs. 29–34. Stages in longitudinal division taken from the same individual. Figs. 35–37. 'Small Ovals.' Fig. 38. Scale of 'Small Ovals'. Fig. 39. Intermediate size between 'Small Ovals' and mature cell. Figs. 40, 41. 'Small Spheres.' Fig. 42. Scales of 'Small Spheres'. Figs. 43–46. 'Small Sphere' liberating its contents which divide, taken from same cell. Fig. 47. Precyst stage. Figs. 48–51. *M. lychenensis*. Fig. 48. Shedding of the scales. Figs. 49, 50. Small individuals. Fig. 51. Precyst stage also showing shedding of the scales. × 1000.

the immediate separation of the liberated protoplast into two parts suggests that it had actually divided before it left the cell armour. The two protoplasts seen in Fig. 46 bear a resemblance to the young cell in Fig. 35.

Stage 6. *Precyst stage.* Individuals of var. *gesticulans*, stages 1 to 5, were all abundant during the first 10 days of the swarming period. After this they became relatively rare but the mature ones became more abundant, and the average size of the population gradually increased. Large round leucosin bodies, associated with strings of globules, became very conspicuous and four chromatophore lobes were often present (Fig. 47), see also Fig. 51 of *M. lychenensis* and Fig. 52 of *M. teilingii.*

Stage 7. *Cyst formation.* Cyst formation was studied most fully in *M. teilingii* (Figs. 52–58), but follows the same course in all species. The membrane of the developing cyst is formed within the protoplast of the mother cell and the protoplast passes into it through the pore, which in *M. teilingii* is anterior. This type of reproduction is common among the Chrysophyceae, and has been observed for *Mallomonas* by Carter (1937). As the protoplast passes through the pore it is surrounded on the outside by a covering of foamy cytoplasm full of small contractile vacuoles (Fig. 55). The membrane of the incipient cyst usually becomes thickened early and may show the mature ornamentation before the protoplast has entered it (Fig. 55), but in other cases the membrane remains thin until after the contents have entered it and the thickening and ornamentation presumably occur later (Fig. 57). Fig. 56 shows an intermediate condition.

The fully formed cyst may contain two or four chromatophore lobes (see Fig. 58, of *M. teilingii* with two lobes and Fig. 8 of *M. leboimii* with four lobes). I was not able to see whether the lobes were joined. The nucleus was not observed, but Conrad (1914) noted two nuclei in the cyst of *M. mirabilis.*

Protoplasmic structure

A number of features can be distinguished in the living *Mallomonas* cell.

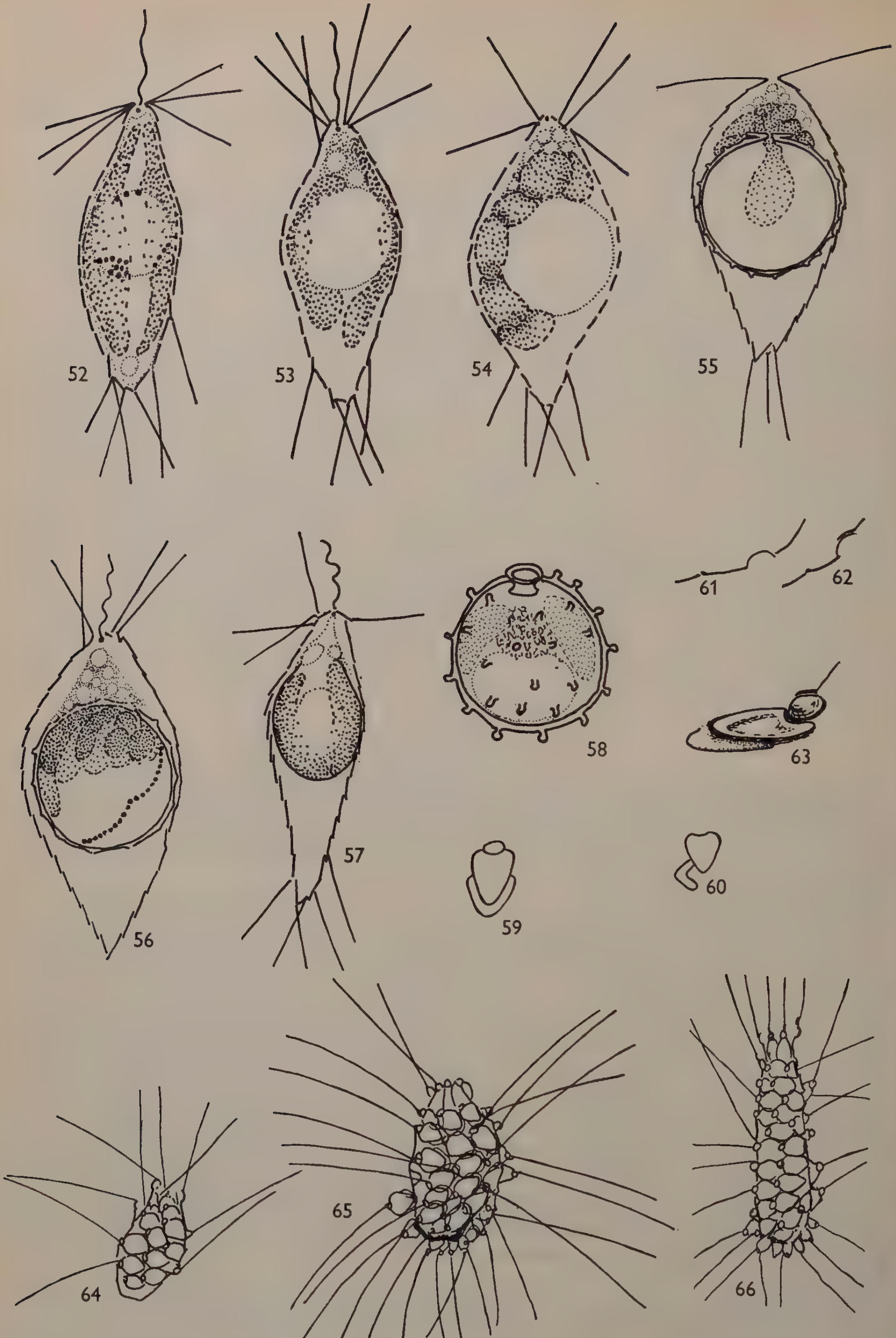
The flagellum arises from a small granule which is situated outside the main protoplasm of the cell. This is the 'perle' of Bourrelly & Chadefaud (1951). The large nucleus, occasionally showing a nucleolus, is usually seen at the anterior end of the cell but is sometimes centrally placed.

The chromatophore is single, deeply divided into two lobes by clefts at the front and rear ends, and in the mature cell is folded round the central cavity of the cell. This is true of all the species which I have examined, some twenty-five. The two lobes may be broad and spirally twisted, completely enveloping the cell as in *M. teilingii* and *M. intermedia* var. *gesticulans* (Figs. 1, 2), or they may be straight as described by Bourrelly (1951) for *M. doignonii.* I have seen individuals of *M. doignonii* where the chromatophore lobes are narrow and almost strap-shaped so that they only occupy one side of the cell. In an immature cell the chromatophore may be smaller (compare Figs. 6 and 17 both of *M. leboimii*, and see also Fig. 16 of an immature *M. lychenensis*). The two lobes may be joined only by an exceedingly narrow bridge of coloured plastid material which is flanked on either side by specialized but colourless protoplasm. This is shown in Fig. 7 for *M. leboimii* and has also been seen in another undescribed species of the same group. Contractile vacuoles are usually situated in the cleft between the lobes and in the space between the free edges of the chromatophores as well as in the extreme rear (Figs. 2, 6 and 17).

This description may be compared with the study of *M. insignis* by Bourrelly & Chadefaud (1951) from which, however, it differs in the interpretation of certain features.

The tripartite scale and bristle

Two of the species described here have a scale which I have called 'tripartite'. There is a large group of species which have this type of scale, including *M. intermedia* and its varieties, and *M. leboimii*, *M. acaroides* and *M. tonsurata* Teiling. The scale



Figs. 52–58. *M. teilingii*. Figs. 52–57. Stages in cyst formation. Fig. 58. Cyst. Figs. 59–66. *M. intermedia* var. *gesticulans*. Figs. 59–63. Tripartite scale. Fig. 59. Isolated scale. Fig. 60. Damaged scale showing detatched flange. Figs. 61, 62. Longitudinal section of scale and bristle with foot in different positions, diagrammatic. Fig. 63. Reconstruction of scale, diagrammatic. Figs. 64, 65, 66. Dried individuals showing arrangement of scales. Fig. 66. Half of bristle only shown. × 1000 except Figs. 59–63. Figs. 59, 60–62, × 2000, Fig. 63, × 4000.

consists of three parts here called the 'shield', the 'dome' and the 'flange'. Fig. 63 shows a diagrammatic reconstruction of the scale, Fig. 59 shows the isolated scale as seen on the slide, Fig. 60 shows a scale in which the dome has been lost and the flange has become detached but lies beside the shield, and Figs. 61, 62 show, diagrammatically, two longitudinal sections through the scale. The shield is a roughly triangular plate of silica, slightly thickened at the edges and somewhat hollowed on its outer side. The dome is a hollow silica hemisphere projecting obliquely outwards from the shield and forming a conspicuous knob in the profile view of the cell. The base, or 'foot', of the bristle comes in contact with the dome, to which it is held, probably by protoplasm, which acts as a hinge and renders the bristle capable of active movement. Sometimes the whole foot is in contact with the dome and sometimes only its tip (Figs. 61, 62). These details may often be seen by focusing on the scales at the anterior end of *M. intermedia* var. *gesticulans* or *M. leboimii* (Figs. 2, 6 and 17). The flange is a delicate silica margin along the two sides of the shield farthest from the dome. It projects obliquely inwards in the intact armour and is entirely covered by the shields of the neighbouring scales. In a dry preparation the dome and flange appear darker than the shield and may for this reason be thought to be thicker, but this dark appearance is due to the angle at which the light strikes the oblique surface, and not, I think, to the thickness of the silica.

In *M. intermedia* var. *gesticulans* and *M. leboimii* the bristle, as has been seen, is joined to the scale by a movable hinge. This hinge is not as clear in all species as it is in those with tripartite scales, but I believe it must exist, in some form, in all bristle-bearing species, since all are able to move their bristles actively. The bristle movements are most striking, however, in the larger species with tripartite scales, and *M. intermedia* var. *gesticulans* was so called because of the way in which it moved its bristles. In a motionless cell most of the bristles radiate, while in a quickly moving cell most trail, as though passively; in both motionless and moving cell, however, one or more bristles may point in a different direction from the rest. Movements are most obvious in such bristles and a forward-pointing bristle may move slowly from side to side as though acting as a feeler. In a stationary cell caught in bits of debris, one sometimes sees a bristle change its position, moving through an angle of 90° in a second or so. Fig. 4 shows the armour of the mother cell with regularly radiating bristles, and may be compared with Figs. 2, 17 (stationary cells) or 21 (moving cell) where the living bristles cross each other and some of the forward-pointing might be expected to show active movement.

A few species of *Mallomonas* possess spines which are quite distinct from bristles, being prolongations of the scale margin, and immovable.

SHEDDING OF SCALES IN MALLOMONAS LYCHENENSIS

M. lychenensis and a small group of allied species, including *M. allorgei* and *M. anglica*, have scales which do not overlap but are joined at the edges to form a rigid armour. Carter (1937) has described how *M. anglica* renews its armour from within, leaving fragments of the old armour adhering to its outer membrane. The same process may be seen in *M. lychenensis*, sometimes a single scale or group of scales is shed and sometimes the whole armour is thrown off (Figs. 48, 51). The process occurs chiefly during the swarming season, probably because this is a time when cells change their shape rapidly, either by growth in length or by the development of leucosin bodies within the cell. I have seen the same sort of shedding of scales in another species (undescribed), of the same group, and should expect it to occur in *M. allorgei* which however is not common in this district.

SCALE ARRANGEMENT

The scales of the *Mallomonas* armour vary in size and sometimes shape, according to their position on the cell, and will be referred to as the 'anterior' scales, immediately surrounding the flagellum, the 'body' scales, over the greater part of the cell and 'posterior' scales, at the extreme rear.

The anterior scales may differ more or less from the body scales and are a useful diagnostic feature. In *M. teilingii* they differ only in bearing bristles, being indistinguishable in size and shape from the body scales, in *M. lychenensis* the anterior scales are highly specialized in shape and are the only scales to bear bristles, while in *M. intermedia* var. *gesticulans* and in *M. leboimii* they tend to be slightly larger than the body scales, the domes point forwards instead of across the cell (Figs. 65, 66), but they show no sharp distinction from the scales immediately behind them.

The anterior scales are the first to be developed in the soft-bodied *Mallomonas* of both stages 1 and 2 (Figs. 16–19, 28), and may develop to their mature size even in quite small cells (Figs. 49, 50) in certain species, while in other species they remain comparatively small in the immature cells as in *M. intermedia* var. *gesticulans*.

The body scales are the most easily seen of all the scales and therefore the chief diagnostic feature. They may be nearly uniform in size all over the cell as in *M. lychenensis* (Figs. 9, 48–50), or they may be larger in front than in the rear as in *M. intermedia* var. *gesticulans*.

The rear scales are minute and may form a group sharply differentiated from the body scales, both in size and shape, as in *M. lychenensis*, or they may intergrade into the body scales as in *M. intermedia* var. *gesticulans*. They are too small to have much diagnostic value.

PARASITES

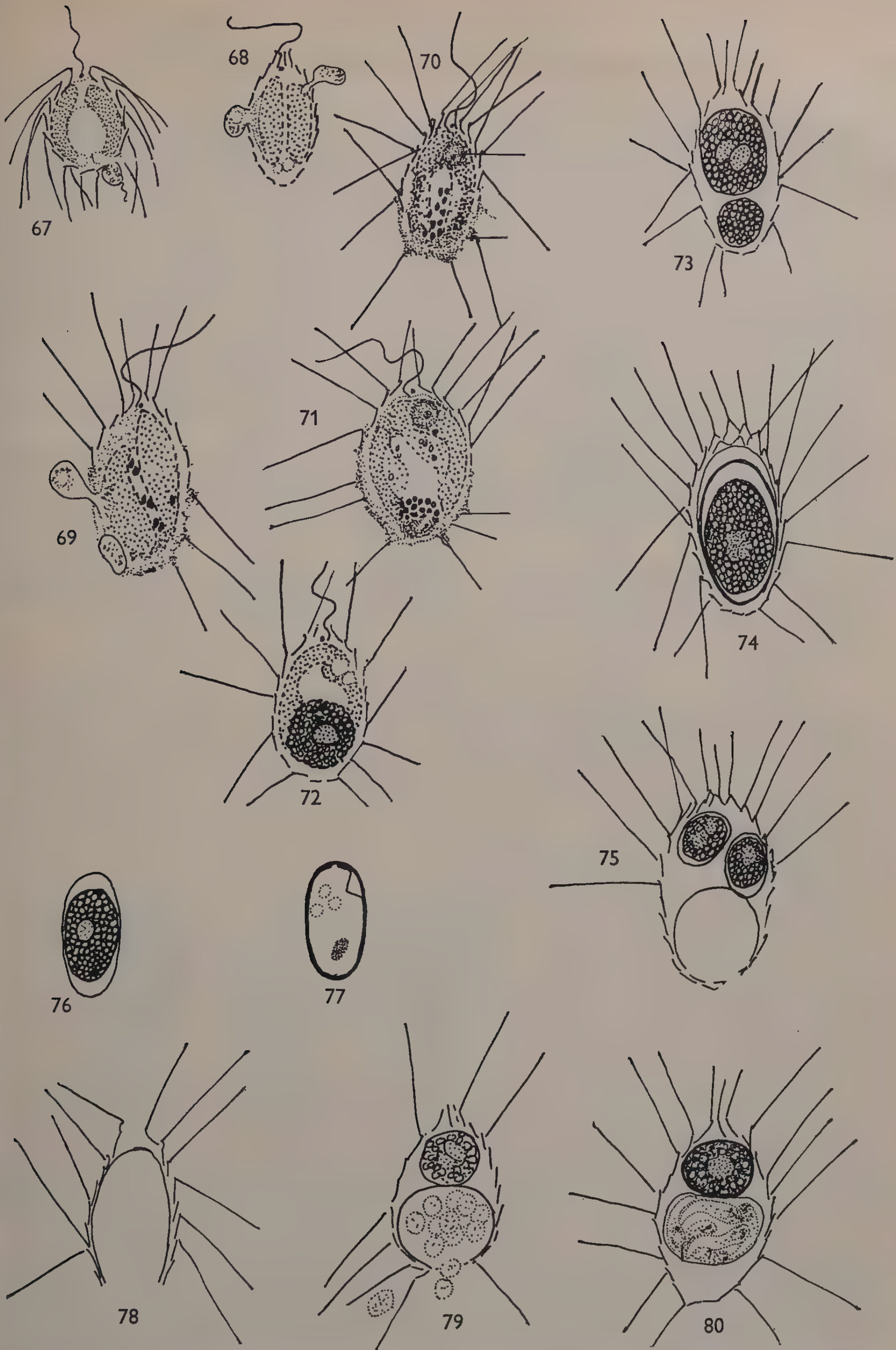
Mallomonas is subject to a number of parasites. The two which I have studied are of importance because they may devastate a population and because certain infected individuals have been mistaken for normal stages of *Mallomonas* development.

Parasite of Mallomonas intermedia *var.* gesticulans

In warm weather in early June large quantities of *M. intermedia* var. *gesticulans*, infected by a parasite, were found in a shallow pond. Samples of this pond were examined daily for 6 days, by which time nearly all the *Mallomonas* and the parasite had encysted. Almost the whole population was devastated by this parasite, only three or four normal cysts being found among many hundreds of parasite cysts. In another pond, some weeks earlier, and in cooler weather, a few early stages of the parasite were found on the same species of *Mallomonas*. Here the attack proved abortive, only the early stages and no cysts being observed, while the *Mallomonas* developed normally.

A similar parasite has been observed on another strain of *M. intermedia* (undescribed). Teiling (1946, pp. 70 and 86) gives a figure and description of a 'dauerspore' in *M. elongata* Reverdin which I believe to be a parasite cyst allied to the one described here.

The parasite was first seen as a colourless nearly spherical zoospore which swam up to the *Mallomonas*, always an immature specimen, and sought to attach itself with rapid jerky movements, the rear of the parasite being in contact with the *Mallomonas* (Fig. 67). This stage was not observed in detail, and only a few examples were seen. An early stage of infection is seen in Fig. 68 and here the parasite is a long oval colourless organism, narrowing to a neck where it is attached to the host. The parasite cytoplasm passes through the cell armour into the cytoplasmic lining, where it spreads. keeping outside the chromatophores. Later it spreads outside the armour as well as inside it, obliterating the scales and bristle bases (Figs. 69, 70). It seems to spread mostly towards the rear of the cell, and when the parasite cytoplasm reaches this end it grows inwards between the lobes of the chromatophore and forms a coarsely granular mass (Figs. 71, 72). The finely granular cytoplasm on the outside of the armour now withdraws into the cell, where the parasite grows, gradually filling the space and digesting the chromatophore. One to three parasites may attack a single host. When nearly full-grown the parasite forms a round or oval body surrounded by a thin wall (Figs. 73, 75). From this stage three types of development appear to be possible.



Figs. 67–80. *M. intermedia* var. *gesticulans* infected by parasite. Fig. 67. Motile parasite attacking *Mallomonas* cell. Fig. 68. Two attached parasites spreading outside chromatophores. Figs. 69, 70. Parasite spreading all through cell and outside armour. Figs. 71, 72. Parasite forming granular mass at base of cell. Fig. 73. Immature parasite cyst. Figs. 74, 75. Mature parasite cysts type I. Fig. 76. Isolated parasite cyst type I. Fig. 77. Empty shell of cyst type I. Fig. 78. *Mallomonas* armour vacated by parasite cyst. Fig. 79. Parasite cyst type 2; with non-motile reproductive bodies. Fig. 80. Parasite cyst type 3, with motile reproductive bodies. ×1000.

Type 1. The commonest type of development is for the protoplasm to contract away from the thin wall and form a second thicker wall, after which it contracts a little further leaving a space at both ends (Figs. 74, 75). Both this space and the one between the walls appear to be full of water. The protoplasmic mass is closely packed with refractive granules and shows one or two brown bodies in the middle, which are the remnants of the chromatophores. The inner wall and its contents form a sporangium which is liberated, leaving the outer wall inside the *Mallomonas* cell wall (Figs. 75, 78). The fate of the sporangium is unknown but occasionally, at any rate, it bursts, liberating its contents, since a number of empty shells were found in the water. Three small colourless spheres and the remnants of the chromatophore were found in one of these empty shells (Fig. 77).

Type 2. In a few individuals the protoplasm, after forming its first wall, divides into a large number of colourless spheres. These were observed to escape as non-motile bodies (Fig. 79). Their further development is unknown.

Type 3. In a single individual the parasite, after forming its first wall, gave rise to six actively motile zoospores which moved rapidly round the cavity. They remained enclosed for about 10 minutes when the individual was lost. It was impossible to see their flagellum (Fig. 80).

It would be reasonable to regard types 2 and 3 as sporangia furnishing soft-bodied reproductive units for rapid reproduction. The possibility also exists that one or more different parasites may be present and produce different types of sporangium.

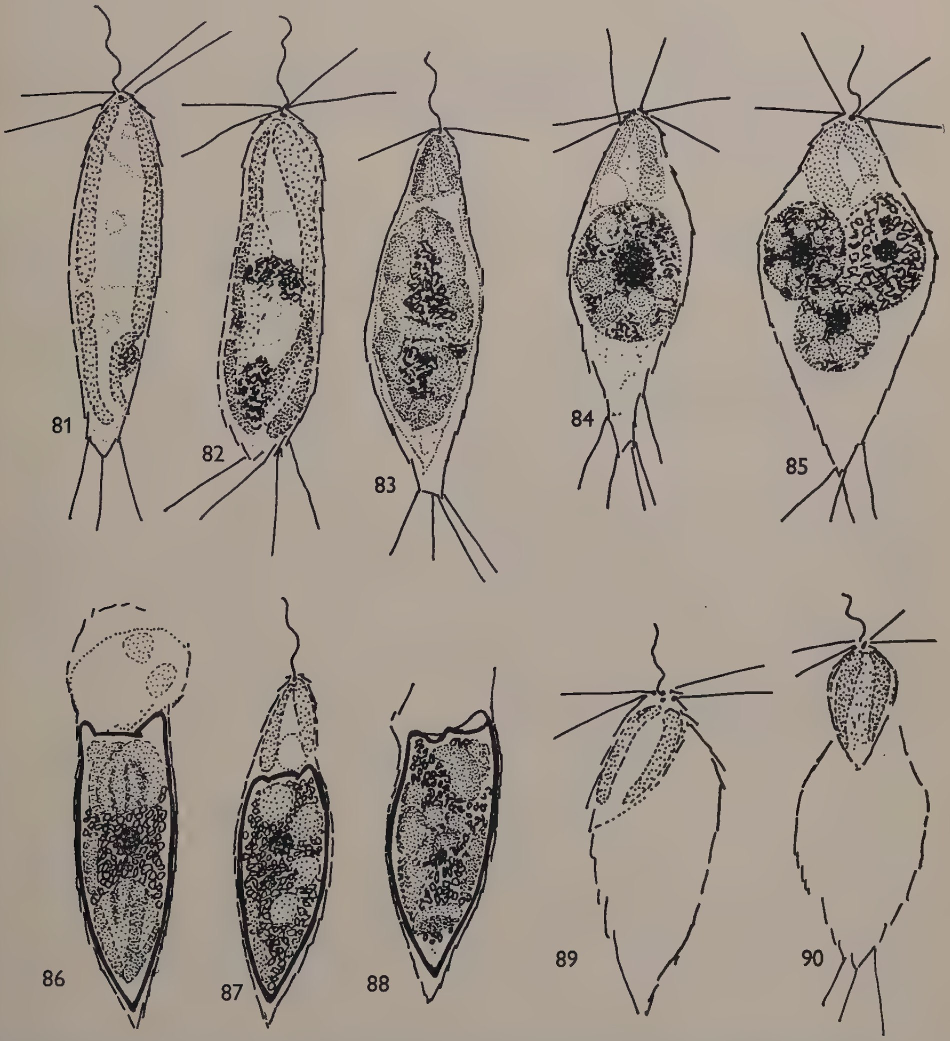
The parasite of Mallomonas teilingii

A few infected individuals are usually to be found in any large population of *M. teilingii*, and occasionally the parasite becomes epidemic and may destroy the greater part of the population. I first mistook this parasite for a stage in the life history of *M. teilingii*, and the mature cysts have been described by Nygaard (1949) under the name of *M. tridentata*. He did not, however, see the early stages of development, and from a study of this and comparison with the normal cyst development, it is clear that the condition is an abnormal one due to a parasitic infection.

The first sign that something is wrong with the cell of *M. teilingii* is shown by the breaking and folding of the chromatophores, the presence of one or more groups of granules in the cell, and the division of the cytoplasm into two or more parts. Fig. 81 shows this, each of the three portions into which the cell is divided has a central body which suggests a nucleus, but I hesitate to call it one. As the condition advances granules collect in groups in the rear divisions of the cell; the front division is usually free from these granules (Fig. 82). The apparently uninfected portion at the anterior end then becomes separated from the rest (Fig. 83), and the infected portion forms one, two or three ovals or spheres according, probably, to the number of infections (Figs. 84, 85). Each sphere or oval consists of a central mass of granules surrounded by broken portions of the chromatophores, which may become disk-shaped and be interspersed with scattered granules. There is no rigid wall as yet round the parasite. When three spheres are present they may be arranged as shown in Fig. 85, or in a single row. The anterior portion of the cell remains separate with an active flagellum and frequently contains a leucosin body at its base. The infected portion now elongates and surrounds itself with a thick wall of the shape shown in Figs. 86–88 which may be called the *tridentata cyst*. The anterior portion of the original *Mallomonas* may die, as shown in Fig. 86, or may continue to live. Fig. 89 shows this portion attached to an empty *Mallomonas* armour from which the tridentata cyst has escaped, and Fig. 90 shows it escaping from such an armour. I have never seen the condition with two or three infections develop beyond the stage shown in Fig. 85, but I have seen the infected portions burst the armour and escape at about this stage, and I think it possible that they may continue their development in the water.

A very similar parasite attacks *M. heterospina*, but as I have not seen the resting cyst I cannot say whether it is the same species.

Nygaard (1949, p. 135, fig. 71) shows an incompletely described species referred to as *N.sp.I*, which, from the figures, appears to be infected by a parasite of the *tridentata* type. No cyst is shown, but the shape of the anterior portion of the cell contents of several cells recalls Figs. 83 and 84 of *M. teilingii*.



Figs. 81–90. *M. teilingii* infected by parasite. Figs. 81–85. Stages after infection. Figs. 86–88. Mature cyst. In Fig. 86, the *Mallomonas* protoplasm has died; in Fig. 87 it is still active. Figs. 89, 90, escape of remnant of *Mallomonas* protoplasm.

I think that both the parasite of *M. intermedia* var. *gesticulans* and of *M. teilingii* need further study before they can be classified. In both, the chromatophore is taken into the body of the parasite and this is distinctly a feature of a Protozoa rather than a unicellular fungus.

Summary

1. Certain aspects of the ecology, structure and life history of four species of *Mallomonas* are described.

2. *M. intermedia* Kisselew var. *gesticulans* var. nov. and the cyst of *M. leboimii* Bourrelly are described.

3. The chromatophore in all four species is single and deeply lobed.

4. Several stages of the life cycle of *M. intermedia* var. *gesticulans* and *M. lychenensis* Conrad are described (some of them seem to be new), and also cyst formation in *M. teilingii* Conrad.

5. The tripartite scale and bristle attachment, and also the movement of bristles, are described for *M. intermedia* var. *gesticulans*.

6. The scale arrangement is described for *M. intermedia* var. *gesticulans* and *M. lychenensis* Conrad, and the shedding of the scales for *M. lychenensis*.

7. Two internal parasites are described, one affecting *M. intermedia* var. *gesticulans* and one affecting *M. teilingii*.

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The Combretum species of the New World. By A. W. Exell.

(With 5 Text-figures)

[Read 7 May 1953]

The work here published was nearly completed before the outbreak of war in 1939 as part of a larger project embracing the whole family of Combretaceae in the Western Hemisphere. Owing to other commitments I now find it impossible to finish the whole work or even to bring that part of it dealt with here up-to-date by studying the collections which have doubtless been received by American and Continental European herbaria since 1939. It seems worth while, however, to publish this account of the American species of *Combretum* for, in spite of its deficiencies and the many problems it leaves unsolved, it may provide a temporary basis for arranging material in herbaria and a foundation for further work on the genus.

The classification proposed by Engler and Diels (in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii (1899)) has been followed here with a few modifications. The principal changes are: (1) the union of sections *Discolores* Engl. & Diels and *Mellifluae* Engl. & Diels under the former name; (2) the union of sections *Monetariae* Engl. & Diels and *Anfractuosae* Engl. & Diels under the former name; (3) the substitution of the earlier name Sect. *Eucombretum* Don for Sect. *Micropetalae* Engl. & Diels; (4) the union of sections *Combretastrum* Eichl. and *Olivaceae* Engl. & Diels (composed of African species) under the former name; (5) the description of a new section *Spinosae* based on *C. spinosum* Bonpl.; and (6) the maintenance of *C. rupicola* Ridl. in the section *Terminaliopsis* proposed for it by Ridley.

The species problem in the genus *Combretum* is nearly as difficult in the American species as in the African ones, where it has long been recognized but never satisfactorily solved. All that it seems possible to do, at present, in the case of a presumably heterogeneous population in which there appears to be a constant reshuffling of genes, so that a number of characters occur in nearly every possible combination, is to give the 'complex' the earliest legitimate name available and append a synonymy that is nearly always a long one, due to the many diverse elements included. It should be realized that the synonyms fall into three categories: (1) nomenclatural synonyms indissolubly linked with the accepted name; (2) names given to plants which appear to be identical with the type; and (3) names given to plants which differ in certain characters from the type but each of which represents one combination of a number of characters that combine in numerous ways within a heterogeneous population. Whether or not any particular instance in this third category should be considered worthy of specific or infra-specific rank must be a matter of individual judgement or even of convenience; but it should be borne in mind that we are at present completely ignorant of the genetic structure and it seems better not to propose a classification which implies far more knowledge than we possess. Many such combinations of characters have been given specific or infra-specific epithets by various authors, but it is often evident that there is almost no end to such a process and that a synthesis is more convenient and perhaps more in accordance with the truth. Such a synthesis is no reflexion on the work of the original authors, who described the differences that they saw. The words 'convenience' and 'convenient' are used deliberately. Until it becomes possible (if ever) to give to plants 'chromosome maps', equivalent, in a way, to the formulae employed by chemists, it seems best to deal with these heterogeneous populations, within the framework of the International Rules of Nomenclature, in whatever manner seems most practically convenient.

The two major problems concerning the New World species of *Combretum* are in sections *Eucombretum* and *Combretastrum*. In each of these a large number of taxa have been here united in a 'complex' or very polymorphic species, while a few taxa, slightly more divergent from the types, have been retained as species. Several such taxa are so imperfectly known that their status is uncertain.

In the case of *Combretum laxum* Jacq. (Sect. *Combretastrum*), an attempt was made to describe the various combinations of characters as subspecies or varieties and of these about sixteen could be recognized. As, however, some of these were based on fruit and others on flower characters, the fact that very few individuals have been collected in both flower and fruit made the classification of very doubtful practical convenience and it was abandoned.

As to the relationship of the sections, there can be no certainty, but a few guesses can be made. In the arrangement used in this work, sections 1–8 seem to show a certain relationship, the upper receptacle elongating from the shallowly cupulate shape, in Sect. *Parviflorae*, to the well-developed, slightly asymmetric tube of Sect. *Cacoucia*. Sections 9–11 seem also to be interrelated and somewhat separated from the others, their nearest allies being in tropical Africa. The difference between tetramerous and pentamerous flowers is clearly of no fundamental importance in assessing relationship, the two sections with normally pentamerous flowers, *Cacoucia* and *Spinosae*, showing no evidence of close affinity. A little more needs to be said, however, concerning tetramery in the genus. As *Terminalia* and *Combretum* are clearly closely related and as the flower in *Terminalia* is remarkably constant, we should expect the most primitive type of flower in *Combretum* (or at least the type of flower which existed when the two genera diverged) to be *Terminalia*-like, i.e. with a shallow-cupulate receptacle, and pentamerous. In *Combretum*, however, the species with this type of receptacle (and with even flatter ones) are mainly tetramerous. *Strephonema*, the most primitive genus known in the Combretaceae, with the ovary only semi-inferior, has a cupulate receptacle and pentamerous flowers. One can do no more than emphasize the fact, already stressed by Engler and Diels, that in *Combretum* the flower has undergone striking modifications in various directions, the fruit remaining relatively constant, while in *Terminalia* the flower shows little variation but the fruit shows great range of form.

The relationship between the American and African species of *Combretum* is evident and interesting. Sect. *Cacoucia* occurs in tropical America from British Honduras to Brazil and also in western tropical Africa. Sect. *Combretastrum* does not differ fundamentally from Sect. *Olivaceae* and their union gives a second section with a transatlantic distribution. Sect. *Elegantes*, from Brazil and eastern Peru, shows a close resemblance to Sect. *Tomentosae* Engl. & Diels, from western tropical Africa, while Sect. *Parviflorae* shows clear affinity with the African section *Hypocrateropsis* Engl. & Diels. Sect. *Eucombretum*, restricted to the New World, seems to be paralleled by sections *Ciliatipetalae* Engl. & Diels and *Glabripetalae* Engl. & Diels in tropical Africa, but with a fairly considerable divergence. As usual, the rain-forest (and mangrove)[1] species show much closer transatlantic affinities than do elements of the savanna floras, which are more recent in origin.

The presence of Sect. *Cacoucia* on both sides of the Atlantic is a noteworthy feature. The species of this section must rank among the most highly developed in the genus, and even if *Cacoucia* Aubl. be maintained as a separate genus the distributional problem remains substantially the same. Three hypotheses require consideration: (1) almost the whole process of evolutionary development took place while there was still a land-bridge between South America and Africa, or while the continents were united (Continental Drift Theory), or at least while they were near enough for intercontinental dispersal to occur (perhaps in the Eocene); (2) parallel evolution has taken place in America and Africa; (3) the South Atlantic is not an effective barrier.

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[1] *Laguncularia racemosa* Gaertn. f., a mangrove belonging to the Combretaceae, is common to tropical America and western tropical Africa.

It is difficult to believe that the main evolutionary development in the genus, which itself belongs to a far from primitive family, was completed before the postulated separation of South America and Africa and that the genus has remained at a standstill ever since. The disjunction of the two continents at the evolutionary level represented by sections *Parviflorae-Hypocrateropsis* (America and Africa respectively) and *Combretastrum* (in both continents) would appear more probable; but it is difficult to accept, as a corollary to this, that Sect. *Cacoucia* shows a parallel realization of evolutionary potentialities on both sides of the Atlantic, for the American and African species of the section resemble each other closely in leaf as well as flower characters.

ABBREVIATIONS USED FOR HERBARIA CITED

BM	British Museum, London
Br	Brussels, Jardin Botanique de l'État
Caen	Caen, Jardin Botanique
Cop	Copenhagen, Universitetets Botaniske Museum
DC	De Candolle's Herbarium, Geneva
Go	Göttingen, Botanische Anstalten der Universität
K	Kew, Royal Botanic Gardens
Ley	Leyden, Rijksherbarium
Mu	Munich, Botanische Anstalten
NY	New York Botanical Garden
P	Paris, Muséum National d'Histoire Naturelle
	PHB Herb. Bonpland
	PHC Herb. Cosson
	PHD Herb. Drake
	PHJ Herb. Jussieu
	PHL Herb. Lamarck
ST	Stockholm, Naturhistoriska Riksmuseet
US	United States National Herbarium, Washington
Ut	Utrecht, Botanisch Museum en Herbarium
VH	Van Heurck's Herbarium, Antwerp

Combretum Loefl.

Loefl., *Iter Hispan. App.*: 308 (1758)

The genus is based on a specimen collected by Loefling in tropical South America, evidently the same specimen as that described by him as *Gaura fruticosa* (tom. cit.: 248 (1758)). The name *Combretum*, which is antedated by *Grislea* L. (1754), has been conserved.

ARTIFICIAL KEY TO THE SECTIONS

- Flowers symmetric, medium to small; upper receptacle rarely exceeding 1 cm. in length (measuring to the tips of the calyx-lobes).
  - Flowers tetramerous.
    - Petals present.
      - Upper receptacle shallow-cupuliform; stamens shorter than the petals; flowers very small. 1. *Parviflorae.*
      - Upper receptacle cupuliform to narrowly infundibuliform; stamens longer than the petals.
        - Petals densely hairy; flowers small; upper receptacle not exceeding 3·5 mm. long (from the base of the style to the tips of the calyx-lobes).
          - Leaves densely tomentose beneath. 4. *Elegantes.*
          - Leaves minutely puberulous or almost glabrous beneath. 11. *Spinosae.*
        - Petals glabrous or slightly pubescent, if densely hairy then flowers fairly large with upper receptacle exceeding 5 mm. in length (from the base of the style to the tips of the calyx-lobes).

Disk well-developed, margin pilose.

Upper receptacle produced well beyond the disk, the petals being inserted at least 2 mm. above the margin of the latter; petals elliptic, obovate or suborbicular.

Petals at least twice as long as the calyx-teeth; flowers in terminal spikes. 6. *Frangulifoliae.*

Petals scarcely exceeding or shorter than the calyx-teeth.

Flowers in fairly stout lateral spikes. 7. *Eucombretum.*

Flowers in terminal or lateral panicles. 5. *Leprosae.*

Upper receptacle not produced far beyond the disk, so that the petals are inserted less than 1 mm. above the margin of the latter; flowers in panicles or small, slender spikes; petals cuneate.

Flowers less than 4·5 mm. long from the rhachis to the tips of the calyx-lobes; disk without a distinct, free margin. 2. *Discolores.*

Flowers 5 mm. or more from the rhachis to the tips of the calyx-lobes; disk with distinct, free margin. 3. *Monetariae.*

Disk inconspicuous, glabrous; flowers small, usually in terminal panicles. 9. *Combretastrum.*

Petals absent. 10. *Terminaliopsis.*

Flowers pentamerous.

Petals exceeding the calyx-lobes. 11. *Spinosae.*

Petals shorter than the calyx-lobes. 4. *Elegantes.*

Flowers slightly asymmetric, comparatively large, pentamerous; upper receptacle somewhat curved, about 1·5 cm. in length to the tips of the calyx-lobes; fruit 5-ridged. 8. *Cacoucia.*

CONSPECTUS OF THE SECTIONS

SERIES 1. *Flowers* tetramerous. *Upper receptacle* patelliform to infundibuliform, scaly. *Petals* obovate, cuneate or narrowly cuneate, exceeding the calyx-lobes, glabrous. *Disk* campanulate to infundibuliform with a pilose margin.

1. Sect. PARVIFLORAE Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 9, 103 (1899). Based on *Combretum parviflorum* Eichl.

DESCRIPTION. *Woody climbers. Flowers* tetramerous, small. *Upper receptacle* shallow-cupuliform, conspicuously scaly on the outside. *Petals* spathulate to obovate, apically emarginate, glabrous. *Disk* patelliform, pilose at the margin. *Stamens* 8, shorter than the petals, scarcely exserted beyond the calyx-lobes. *Fruit* 4-winged.

DISTRIBUTION. One species in Brazil and Bolivia.

This is closely related to Sect. *Hypocrateropsis* Engl. & Diels from tropical Africa but differs in the rather more distinctly cupulate upper receptacle and the emarginate petals.

2. Sect. DISCOLORES Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 9, 104 (1899). Based on *Combretum discolor* Taub.

Sect. *Mellifluae* Engl. & Diels, tom. cit.: 10, 108 (1899). Based on *Combretum mellifluum* Eichl. and *C. blanchetii* Eichl.

DESCRIPTION. *Small shrubs* (always ?). *Flowers* tetramerous, small. *Upper receptacle* shallow-cupuliform at the apex with a short, infundibuliform base containing the disk, conspicuously scaly on the outside. *Disk* shortly infundibuliform, pilose on the margin. *Petals* spathulate, glabrous. *Stamens* usually 8 (rarely up to 16), exserted, exceeding the petals. *Fruit* 4-winged.

DISTRIBUTION. Two species in Brazil, one of them extending to Paraguay.

3. Sect. MONETARIAE Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 10, 108 (1899). Based on *Combretum monetaria* Mart. and *C. pisonioides* Taub.

Sect. *Anfractuosae* Engl. & Diels, tom. cit. 10, 108 (1899). Based on *Combretum anfractuosum* Mart.

DESCRIPTION. *Erect shrubs* or *small trees. Flowers* tetramerous. *Upper receptacle* cupuliform at the apex with a narrowly infundibuliform base containing the disk. *Petals* obovate to spathulate, glabrous. *Disk* narrowly infundibuliform with pilose margin. *Stamens* 8, exserted, longer than the petals. *Style* exserted. *Fruit* 4-winged.

DISTRIBUTION. Three species in Brazil, one of them extending to Bolivia and Paraguay. The constrictions of the fruit, which led Engler and Diels to propose a separate section for *C. anfractuosum*, are probably due to galling.

SERIES 2. *Flowers* usually tetramerous. *Upper receptacle* cupuliform, densely tomentose. *Petals* obovate-spathulate, hairy, shorter than the narrowly triangular, very acute calyx-lobes.

4. Sect. ELEGANTES Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 9, 104 (1899). Based on *Combretum elegans* Cambess. and *C. floccosum* Eichl.

DESCRIPTION. *Woody climbers. Flowers* tetramerous (or rarely pentamerous). *Upper receptacle* shallow-cupuliform at the apex with a short, cupuliform base containing the disk, densely tomentose. *Petals* obovate-spathulate, tomentose, shorter than the calyx-lobes, the latter narrowly triangular and unusually long for the genus. *Disk* cupuliform with a free, pilose margin. *Stamens* usually 8, exserted. *Style* exserted. *Fruit* unknown.

DISTRIBUTION. One species in Brazil and eastern Peru.

SERIES 3. *Flowers* usually tetramerous. *Upper receptacle* campanulate to elongate-campanulate, sometimes with a distinct, infundibuliform, basal region containing the disk, glabrous or pubescent, usually scaly on the outside. *Petals* obovate, suborbicular, elliptic or narrowly elliptic, not greatly exceeding the calyx-lobes (except in Sect. *Frangulifoliae*), rarely absent. *Disk* infundibuliform or broadly infundibuliform, margin pilose, rarely distinctly free.

5. Sect. LEPROSAE Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 10, 110 (1899). Based on *Combretum leprosum* Mart. and *C. leptostachyum* Mart.

DESCRIPTION. *Erect shrubs* or *small trees* (sometimes climbing?). *Flowers* tetramerous. *Upper receptacle* elongate-campanulate, conspicuously scaly on the outside. *Petals* suborbicular, equalling or slightly exceeding the calyx-lobes, glabrous. *Disk* well-developed, infundibuliform with pilose margin. *Stamens* 8, exserted, exceeding the petals. *Style* exserted. *Fruit* 4-winged.

DISTRIBUTION. One species in Brazil, Bolivia and Paraguay.

6. Sect. FRANGULIFOLIAE Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 10, 110 (1899). Based on *Combretum frangulifolium* Kunth.

DESCRIPTION. *Flowers* tetramerous. *Upper receptacle* campanulate, conspicuously scaly on the outside. *Petals* obovate, rather large, much exceeding the calyx-lobes. *Disk* broadly infundibuliform with pilose margin. *Stamens* 8, exserted, exceeding the petals. *Style* exserted. *Fruit* rather narrowly 4-winged, pyramidal.

DISTRIBUTION. One species in Colombia?, Venezuela and Trinidad.

7. Sect. EUCOMBRETUM Don, *Gen. Syst.* ii: 662 (1832). Don's section *Eucombretum* contained all the tetramerous species of the genus known to him. The first species cited is *Combretum secundum* Jacq. and this, being a synonym of *C. fruticosum* (Loefl.) Stuntz, the type species of the genus, must clearly be chosen as the type of the section.

> Sect. *Micropetalae* Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 10, 108 (1899). Based on nine species of *Combretum*, including *C. loeflingii* Eichl. (now *C. fruticosum*). As the name *Micropetalae* is taken from *C. micropetalum* DC. this should be regarded as the type of the section. It is a synonym of *C. fruticosum*.

DESCRIPTION. *Small trees, shrubs* and *woody climbers. Flowers* usually tetramerous, rather large for the genus as represented in America, in stout, lateral spikes. *Upper receptacle* broadly campanulate to elongate-campanulate, often with a distinct, infundibuliform, basal region containing the disk, scaly on the outside (scales sometimes minute), glabrous to tomentose. *Petals* suborbicular to narrowly elliptic, not, or scarcely, equalling the calyx-lobes, glabrous, pubescent or scaly (rarely absent). *Disk* infundibuliform, margin pilose, sometimes free. *Stamens* 8, exserted, much exceeding the petals. *Style* exserted. *Fruit* 4-winged.

DISTRIBUTION. Eleven species: one widespread from Mexico to northern Argentina; two in Central America; one in Venezuela, Guiana, Peru, Bolivia and Brazil; one in Peru and Brazil; one restricted to Colombia and one to French Guiana; two restricted to Peru and two to Brazil.

SERIES 4. *Flowers* pentamerous, slightly asymmetric, large for the genus. *Upper receptacle* broadly campanulate, slightly curved. *Petals* oblong-elliptic to oblanceolate, exceeding the calyx-lobes, pubescent.

8. Sect. CAUCOUCIA (Aubl.) Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 11, 100, 112 (1899). Based on the genus *Cacoucia* Aubl., of which the type species is *C. coccinea* Aubl. (now *Combretum cacoucia* Exell).

DESCRIPTION. *Woody climbers. Flowers* pentamerous, slightly asymmetric, large for the genus. *Upper receptacle* broadly campanulate, slightly curved, sericeous. *Calyx-lobes* triangular, acute. *Petals* oblong-elliptic to oblanceolate, exceeding the calyx-lobes, pubescent. *Disk* cupuliform with pilose margin. *Stamens* 10, exserted, exceeding the petals. *Style* exserted. *Fruit* 5-angled (in the American species).

DISTRIBUTION. One species in tropical America, from British Honduras to Brazil; four others in tropical Africa.

SERIES 5. *Flowers* tetramerous, small, usually in much-branched, terminal and lateral panicles. *Upper receptacle* cupuliform to campanulate. *Petals* suborbicular to reniform, exceeding the calyx-lobes, or absent. *Disk* poorly developed or absent, margin never pilose.

9. Sect. COMBRETASTRUM Eichl. in Mart., *Fl. Bras.* xiv, 2: 115 (1867). Based on *Combretum sprucei* Eichl., *C. jacquinii* Griseb., *C. obtusifolium* Rich., *C. laurifolium* Mart., *C. nitidum* Spruce, *C. phaeocarpum* Mart. and *C. brevistylum* Eichl. Of these, *C. jacquinii* Griseb., a synonym of *C. laxum* Jacq., is selected as the type species of the section.

Sect. *Olivaceae* Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 9, 104 (1899). Based on six tropical African species of which *Combretum olivaceum* Engl. is selected as the type.

DESCRIPTION. *Woody climbers* (rarely erect). *Flowers* tetramerous, small. *Upper receptacle* cupuliform to campanulate. *Petals* reniform, exceeding the calyx-lobes, glabrous. *Disk* usually very small. *Stamens* 8, exserted, exceeding the petals. *Style* usually exserted but very short in *C. brevistylum* and *C. ulei*. *Fruit* 4-winged or 4-angled.

DISTRIBUTION. Ten species in America: one widespread in Central and tropical and subtropical South America; one restricted to Venezuela and one to Venezuela and Guiana; one restricted to British and French Guiana and one to British Guiana; one (insufficiently known) confined to Jamaica; and four restricted to Brazil. There are also about ten species in tropical Africa.

It was my original intention to exclude *C. brevistylum* (and *C. ulei* would have been placed with it) from this section (see Exell in *Lilloa*, v: 126 (1940)), but I now consider this to be inadvisable.

10. Sect. TERMINALIOPSIS Ridl. in *J. Linn. Soc. Bot.* xxvii: 28 (1890). Based on *Combretum rupicola* Ridl.

DESCRIPTION. *Shrub. Flowers* dioecious (male unknown), tetramerous, very small. *Upper receptacle* shallow-cupuliform. *Petals* absent. *Style* exserted. *Fruit* unknown.

DISTRIBUTION. One species in Fernando Noronha.

SERIES 6. *Flowers* usually pentamerous rarely tetramerous, small. *Upper receptacle* cupuliform to campanulate. *Petals* obovate to obovate-spathulate, exceeding the calyx-lobes, hairy.

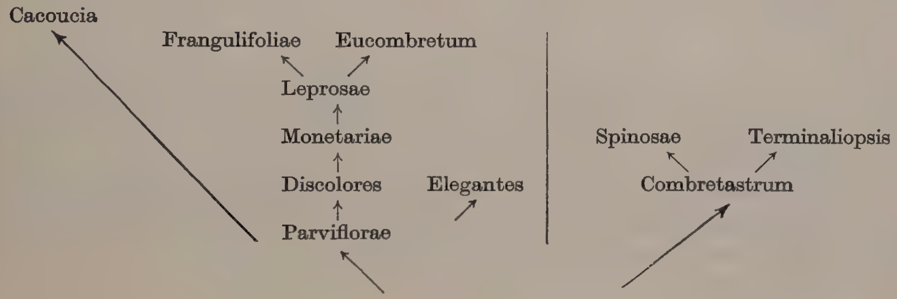
11. Sect. Spinosae Exell.[1] Type species: *Combretum spinosum* Bonpl.

Description. *Woody climbers* or *erect shrubs*. *Flowers* pentamerous (rarely tetramerous), small, in terminal and lateral panicles. *Upper receptacle* cupuliform to campanulate. *Petals* obovate to obovate-spathulate, densely pubescent. *Disk* small, fleshy, surrounding the base of the style. *Stamens* 10 (rarely 8), exserted, exceeding the petals. *Style* exserted. *Fruit* 5-winged (rarely 4-winged).

Distribution. Four species: one from Mexico to Colombia; one in the West Indies and Venezuela; one restricted to Mexico and one to Ecuador.

Relationship of the sections

Sections 1–8 show increasing development of the upper receptacle from the small, shallow-cupuliform type to much larger, infundibuliform and campanulate types, with slight asymmetry in Sect. *Cacoucia*. These do not necessarily constitute a single line of descent, but there are traces of interrelationships such as might be expected in several lines of descent from a common ancestor. Sections 9–11 appear to be interrelated but rather remote from the other New World sections of the genus; so that there is a break between sections 8 and 9.



1. Sect. Parviflorae Engl. & Diels

1. Combretum vernicosum Rusby in *Mem. N.Y. Bot. Gard.* vii: 312 (1927); non *C. vernicosum* Fenzl. (1844) nom. nud. Based on *White 2374*. [Fig. 1*a*.]

Combretum parviflorum Eichl., in Mart., *Fl. Bras.* xiv, 2, 114 (1867); non *C. parviflorum* Reichenb. (1825). Based on specimens collected by Martius in the province of Bahia, by Pohl near Goyaz, and by Riedel at Cuiabá, Matto Grosso.

Distribution. Brazil and Bolivia.

Specimens:

BRAZIL. Goyaz: *Burchell 6719* (K; NY; P; US), *6981* (K), *6999* (K), *7293–2* (K; P). Rio de Janeiro: *Glaziou 14687* (K). Without precise locality: *Riedel 752* (K).

BOLIVIA. R. Ibon, *White 2374* (NY, type).

In flower, this species can readily be distinguished from *C. mellifluum*, which it sometimes closely resembles, by the fact that the stamens are distinctly shorter than the petals while they are longer in *C. mellifluum*.

The *Index Kewensis* attributes *C. parviflorum* Reichenb. to De Candolle, *Prodr.* iii: 21 (1828), where it was cited as a synonym of *C. micranthum* Don, but the name was validly published three years earlier (Reichenb., *Icon. Bot. Exot.*: 46, t. 62 (1825)), thus invalidating *C. parviflorum* Eichl.

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[1] *Combretum* Sect. Spinosae Exell, sect.nov. *Flores* pentameri, parvi. *Receptaculum* superius cupuliforme vel breviter campanulatum. *Petala* obovata vel spathulata, dense pubescentia. *Discus* patelliformis, crassiusculus.

2. Sect. Discolores Engl. & Diels

Key to the species

Leaves opposite; spikes fairly lax.	2. *mellifluum.*
Leaves subverticillate or alternate; spikes dense.	3. *discolor.*

2. **Combretum mellifluum** Eichl. in Mart., *Fl. Bras.* xiv: 2, 113 (1867). Based on *Blanchet 2866* and *Gardner 2159*, of which the former is selected as the type [Fig. 1*b*.]

Distribution. Brazil and Paraguay.

Key to the varieties

Stamens 8.	var. *a. mellifluum.*
Stamens up to 16, in verticils.	var. *b. hyperteleiandrum.*

Var. *a.* **mellifluum**

Combretum blanchetii Eichl. in Mart., *Fl. Bras.* xiv, 2: 114 (1867). Based on *Blanchet 3105.*

Combretum mellifluum var. *cuspidatum* Hassler in Fedde, *Rep. Nov. Spec.* viii: 45 (1910). Based on *Hassler 10737* from Sierra de Ambambay, Paraguay.

Distribution. Brazil and Paraguay.

Specimens:

BRAZIL. Piauhy: *Gardner 2159* (BM; Caen; K; P; PHD), *2160* (P). Bahia: R. S. Francisco, *Blanchet 2866* (Type; BM; K; PHD); Jacobina, *Blanchet 3105* (BM; Caen; K; P; PHD), *3107* (PHD). Minas Geraes: *Glaziou 9793* (Cop; K; P). Without precise locality: *Pohl 1096* (K).

PARAGUAY. Sierra de Ambambay, *Hassler 10737* (Type of var. *cuspidatum*; BM).

Var. *b.* **hyperteleiandrum** Eichl. in Mart., tom. cit.: 113 (1867). Based on a plant collected by Riedel at Camapuan, Matto Grosso, Brazil.

Distribution. Brazil.

Specimens. None seen.

In the absence of flowers this species may readily be confused either with *Combretum vernicosum* or with *Thiloa paraguariensis* Eichl.

3. **Combretum discolor** Taub. in Engl., *Bot. Jahrb.* xv, Beibl. 34: 9 (1892). Based on *Glaziou 13805a* from Matto Grosso, Brazil. [Fig. 1*c*.]

Distribution. South-eastern Brazil.

Specimens:

BRAZIL. Matto Grosso: Serra Ouro Branco. *Glaziou 13805a* (Type; P); S. Anna da Chapada, *Robert 390* (BM), *390b* (BM), *595* (BM).

3. Sect. Monetariae Engl. & Diels

Key to the species

Fruits as broad as long, or broader.	4. *monetaria.*
Fruits longer than broad.	
Leaves up to 5 cm. long; young branchlets glandular.	5. *pisonioides.*
Leaves 6–12 cm. long; young branchlets not, or very sparsely glandular.	6. *duarteanum.*

4. **Combretum monetaria** Mart. in *Flora*, xxiv, Beibl. 2: 2 (1841). Based on specimens collected by Martius near Joazeiro, Bahia, and in the province of Piauhy, Brazil.

Distribution. Brazil.

Specimens:

BRAZIL. Piauhy: *Martius 410*(7) (Mu). Bahia: near Joazeiro, *Martius 410*(7) (BM, fragment; Mu).

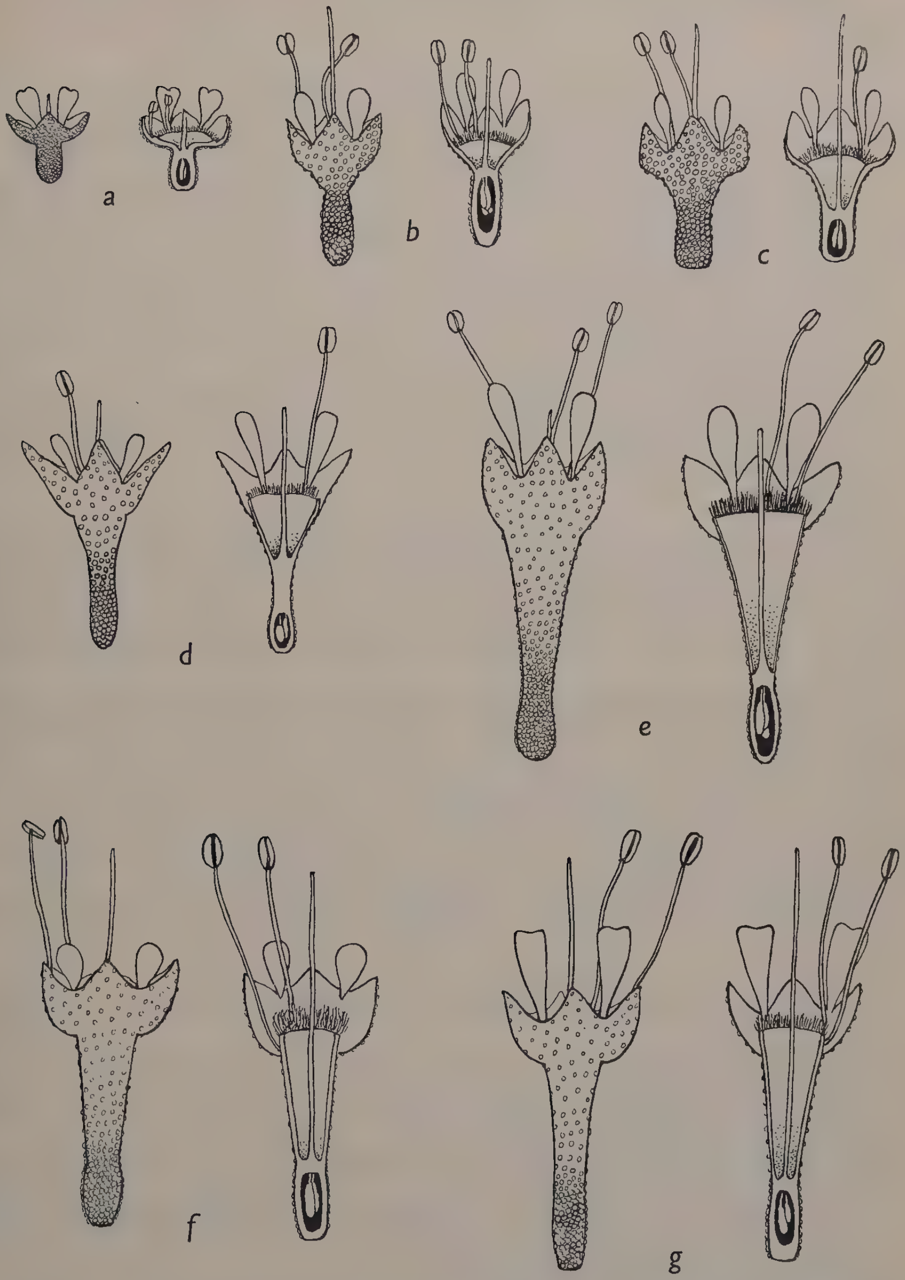

Fig. 1. Diagrams of flower structure. (All × 5.) (*a*) *Combretum vernicosum* Rusby (*Burchell 6719*); (*b*) *C. mellifluum* Eichl. (*Blanchet 2866*); (*c*) *C. discolor* Taub. (*Glaziou 13805a*); (*d*) *C. pisonioides* Taub. (*Glaziou 15325*); (*e*) *C. duarteanum* Cambess. (*Duarte* s.n.); (*f*) *C. duarteanum* Cambess. (*Fiebrig 4041*); (*g*) *C. duarteanum* Cambess. (*Gardner 1593*).

5. **Combretum pisonioides** Taub. in Engl., *Bot. Jahrb.* xv, Beibl. 34: 10 (1892). Based on *Glaziou 15325* and *10713*. [Fig. 1*d*.]

DISTRIBUTION. Brazil.

SPECIMENS:

BRAZIL. BAHIA: 'arbuste cultivé', *Glaziou 10713* (K; P), *10718* (P). RIO DE JANEIRO or MINAS GERAES: 'Environs de Rio Janeiro et d'Ouro Preto', *Glaziou 15325* (K).

6. **Combretum duarteanum** Cambess. in St-Hil., Juss. & Cambess., *Fl. Bras. Merid.* ii: 248 (1829). Based on a specimen collected by Noguera Duarte near Contendas, Minas Geraes, Brazil. [Fig. 1*e–g*.]

Combretum anfractuosum Mart. in *Flora*, xxiv, Beibl. 2: 3 (1841). Based on a plant growing in the province of Piauhy collected by Martius.

Combretum geheebii Heurck & Muell. Arg. in Heurck, *Obs. Bot.*: 223 (1870). Based on *Gardner 1593* from Ceará, Brazil.

Combretum anfractuosum var. *macrostachyum* Hassler in Fedde, *Rep. Nov. Spec.* viii: 45 (1910). Based on *Fiebrig 4041* and *4555* from Aquidaban, Paraguay.

DISTRIBUTION. Brazil, Bolivia and Paraguay.

SPECIMENS:

BRAZIL. PIAUHY: near Correio, *von Lützelburg 1386* (Mu); *Martius 410*(*8*) (Mu). CEARÁ: *Gardner 1593* (BM; Caen; K; P; VH, type of *C. geheebii*), s.n. (K). PERNAMBUCO: *Pickel 143* (BM). GOYAZ: *Burchell 8314* (K). MINAS GERAES: *Duarte* s.n. (P, probably the type). S. Paulo: *Glaziou 10710* (K; P).

BOLIVIA. SANTA CRUZ: S. Ana de Chiquitos, *Herzog 186* (Ley). Without locality: *Glaziou 582* (P).

PARAGUAY. Mountains near R. Apa, *Anisits 2426* (St); Colonia Risso, *Anisits 2493* (St); between R. Apa and R. Aquidaban, *Fiebrig 4041* (BM; Ley; K), *4555* (BM; Ley; K).

The specimen *Duarte* s.n. (P) has lanceolate inflorescential bracts up to 12 mm. long, and at first sight appears different from the rest of the material cited, but unusually large bracts are sometimes met with in other species of the genus and one or two other specimens, such as *Burchell 8314*, show indications of similar bracts.

The three specimens figured show considerable variation, especially in the size and shape of the petals.

4. Sect. ELEGANTES Engl. & Diels

7. **Combretum hilarianum** D. Dietr., *Syn. Pl.* ii: 1303 (1840). Based on *C. elegans* Cambess. [Fig. 2*a*.]

Combretum elegans Cambess. in St-Hil., Juss. & Cambess., *Fl. Bras. Merid.* ii: 247, t. 129 (1829); non *C. elegans* Kunth (1823). Based on a plant growing near Contendas and Lagrador in Minas Geraes, Brazil.

Combretum floccosum Eichl. in Mart., *Fl. Bras.* xiv. 2: 119 (1867). Based on *Blanchet 3261* from Bahia, Brazil.

Combretum pyrenaeum Glaziou in *Bull. Soc. Bot. Fr.* liv, Mém. 3: 204 (1908). Based on *Glaziou 21122* from Goyaz, Brazil.

DISTRIBUTION. Brazil and eastern Peru.

SPECIMENS:

BRAZIL. BAHIA: *Blanchet 2759* (PHD), *3261* (Type of *C. floccosum*; BM; K; P); *Glaziou 10478* (K; P); *Ule 7468* (K). MINAS GERAES: *Clausen 74* (P), s.n. (K); *Glaziou 19143* (K; P); *St-Hilaire* s.n. (P, type). GOYAZ: *Burchell 6573* (K); *Glaziou 21122* (K; P); Queixada, Yatai, *Macedo 1462* (BM). Without precise locality: *Riedel 862* (K; P; US).

PERU. LORETO? Seringal Auristella, R. Acre, *Ule 9666* (K).

Eichler separated *C. floccosum* from *C. hilarianum* mainly on the floccose nature of the indumentum, but this does not appear to be a good specific difference. In some specimens the floccose appearance is found only in certain regions of the leaves and often in localized areas delimited by veins. The cause may be pathological.

5. Sect. LEPROSAE Engl. & Diels

8. **Combretum leprosum** Mart. in *Flora*, xxiv, Beibl. 2: 1 (1841). Based on specimens collected by Martius in the states of Bahia and Piauhy. [Fig. 2*b*.]

Combretum leptostachyum Mart., tom. cit.: 2 (1841). Based on *Martius 577* from Matto Grosso, Brazil.

Combretum hassleranum Chod. apud Chod. & Hassler in *Bull. Herb. Boiss.* Sér. 2, iii: 345 (1903). Based on *Hassler 7617* from Paraguay.

DISTRIBUTION. Brazil, Bolivia and Paraguay.

SPECIMENS:

BRAZIL. MARANHÃO: R. Grajahu, near Timbira, *Krukoff 2041* (K). PIAUHY: Boa Esperança, *Gardner 2161* (BM; Caen; K; P; PHD), s.n. (K); Malhado, *von Lützelburg 442* (BM); *Ule 7467* (K). MATTO GROSSO: *Gaudichaud 179* (P); *Martius 115* (Ley), *577* (BM; Ley; K; P; VH); *Robert 743* (BM; K). RIO DE JANEIRO: *Glaziou 9792* (BM; Cop; P).

BOLIVIA. CHIQUITOS: *D'Orbigny 1017* (P). SANTA CRUZ: *Steinbach 3292* (BM; K), *5117* (NY), *6474* bis (BM; K), *6650* (BM; K), *7479* (BM; K).

PARAGUAY. Between the R. Apa and R. Aquidaban, *Fiebrig 4053* (BM; K); near Concepción, *Hassler 7617* (BM; K; P).

Without locality: *Glaziou 587* (P).

Vernacular name. Mapaiso (Bolivia).

6. Sect. FRANGULIFOLIAE Engl. & Diels

9. **Combretum frangulifolium** Kunth, *Nov. Gen. & Sp. Pl.* vi: 109, t. 538 (1823). Based on a specimen collected by Humboldt and Bonpland in Venezuela on the banks of the R. Orinoco near Angostura and Carichana. [Fig. 2*c*.]

Combretum corylifolium Griseb., *Fl. Brit. W. Ind.*: 711 (1864) nom. nud. Based on a plant collected by Crueger in Trinidad.

Combretum tomentosum Willd. ex Eichl. in Mart., *Fl. Bras.* xiv, 2: 111 (1867) nom. synon.; non *C. tomentosum* Don (1824).

? *Combretum karijonorum* R. E. Schultes in *Bot. Mus. Leafl. Harv. Univ.* xiv: 134, t. 36 (1950). Based on *Schultes 5452* from Vaupes, Colombia.

DISTRIBUTION. Colombia, Venezuela and Trinidad.

SPECIMENS:

COLOMBIA. VAUPES: Macaya-Ajaju river confluence, *Schultes 5452* (Type of *C. karijonorum*, n.v.).

VENEZUELA. BOLIVAR: Angostura (Ciudad Bolivar), *de Grosourdy 13* (P); Ciudad Bolivar, *Holt & Blake 853* (US). AMAZONAS: Puerto Ayacucho, *Holt & Blake 826* (BM); Puerto Ayacucho, *Williams 13035* (K).

WEST INDIES. TRINIDAD: *Purdie* s.n. (K).

Vernacular name. Guayabito or Guayavita (Venezuela).

Schultes 5452 (not seen), the type of *C. karijonorum*, is in fruit. From the illustration, which is said to be natural size but would seem to be × ½ by comparison with the dimensions given in the description, this species appears to be either *C. frangulifolium* or closely related to it.

The specimen collected by Purdie in Trinidad was identified by Grisebach as *C. corylifolium*, of which no description has been published. Although the specimen is very incomplete there is little doubt that it is *C. frangulifolium*.

According to Williams (*Tropical Woods*, 68: 30 (1941)) this is one of the commonest trees along the banks of the Upper Orinoco near the Rapids of Atures.

7. Sect. Eucombretum Don

Key to the species

Receptacle densely tomentose or pilose, indumentum concealing the scales. **10.** *argenteum.*

Receptacle lepidote, glabrous or pubescent but scales always clearly visible.

Calyx-lobes deltoid, not exceeding 4 mm. in length.

Margin of the disk scarcely free, or free for less than 1 mm.

Scales of the inflorescence greyish (at least in dried specimens); upper surface of leaves minutely pustulate; petals about 1 mm. long, usually minutely ciliate, occasionally absent; anthers 1·5–2 mm. long. **11.** *farinosum.*

Scales of the inflorescence golden brown or reddish (in dried specimens).

Scales of inflorescence usually golden brown (in dried specimens); upper surface of leaves sparsely scaly and sometimes minutely pustulate, lower surface usually nearly glabrous, sometimes pubescent; petals usually about 2 mm. long; anthers 1–2 mm. long. **12.** *fruticosum.*

Scales of inflorescence reddish (in dried specimens).

Upper receptacle not swollen at the base.

Upper receptacle infundibuliform, about twice as long as broad; petals 1–2 mm. long; upper surface of leaves minutely pustulate and sparsely scaly. **13.** *rotundifolium.*

Upper receptacle campanulate to campanulate-infundibuliform, about 1½ times as long as broad, suddenly narrowed at the base.

Upper campanulate part of the upper receptacle measuring about 4 mm. from the tips of the calyx-lobes to the base of the bell; upper surface of the leaves rather sparsely and somewhat obscurely lepidote, not pustulate; petals suborbicular. **14.** *rohrii.*

Upper campanulate part of the upper receptacle measuring 6–7 mm. from the tips of the calyx-lobes to the base of the bell; upper surface of the leaves not lepidote.

Petals suborbicular.

Petals less than 1 mm. long; upper surface of leaves minutely pustulate. **15.** *assimile.*

Petals 2 mm. long; upper surface of leaves not pustulate. **16.** *sambuense.*

Petals narrowly to broadly elliptic, 1·5–2 mm. long; leaves sometimes pubescent beneath, especially when young. **17.** *guanaiense.*

Upper receptacle somewhat swollen at the base; petals narrowly elliptic, 1·5 mm. long; upper surface of the leaves densely, minutely pustulate, not lepidote. **18.** *bassleranum.*

Margin of disk free for 2 mm.; leaves fairly densely scaly above and very densely so beneath. **19.** *lanceolatum.*

Calyx-lobes narrowly triangular, 5–6 mm. long; petals narrowly elliptic, 2 mm. long. **20.** *llewelynii.*

10. Combretum argenteum Bertol., *Nov. Comment. Bologna*, iv: 412 (1840). Based on a plant growing at Volcan de Agua, Guatemala. [Fig. 2*d.*]

Combretum erianthum Benth., *Pl. Hartweg.*: 73 (1841). Based on *Hartweg 526* from Retalhulei, Guatemala.

Distribution. From Mexico to Nicaragua.

Specimens:

MEXICO. Oaxaca: Pochutla, *Reko 3523* (US), *3750* (US); Gatulco, *Liebmann 3418* (US).

GUATEMALA. Zacapa: Gualan, *Pittier 1784* (US). Retalhulei: *Bernoulli & Cario 2981* (K); *Hartweg 526* (BM; K, type of *C. erianthum*; P). Escuintla: *Ruano 873* (US). Santa Rosa: Berberena, *J. D. Smith 6230* (US).

HONDURAS. Copan: *Seler 3325* (US). Valle: Tiger Island, Gulf of Fonseca, *Sinclair* s.n. (K).

SALVADOR. Ahuachapan: Ahuachapan, *Standley 20228* (US). San Salvador: *Calderón 355* (US), *1431* (US); Tonacatepeque, *Standley 19452* (US); S. Salvador, *Standley 23126* (US), *23134* (US). San Vicente: Tecoluca, *Shannon 5039* (US).

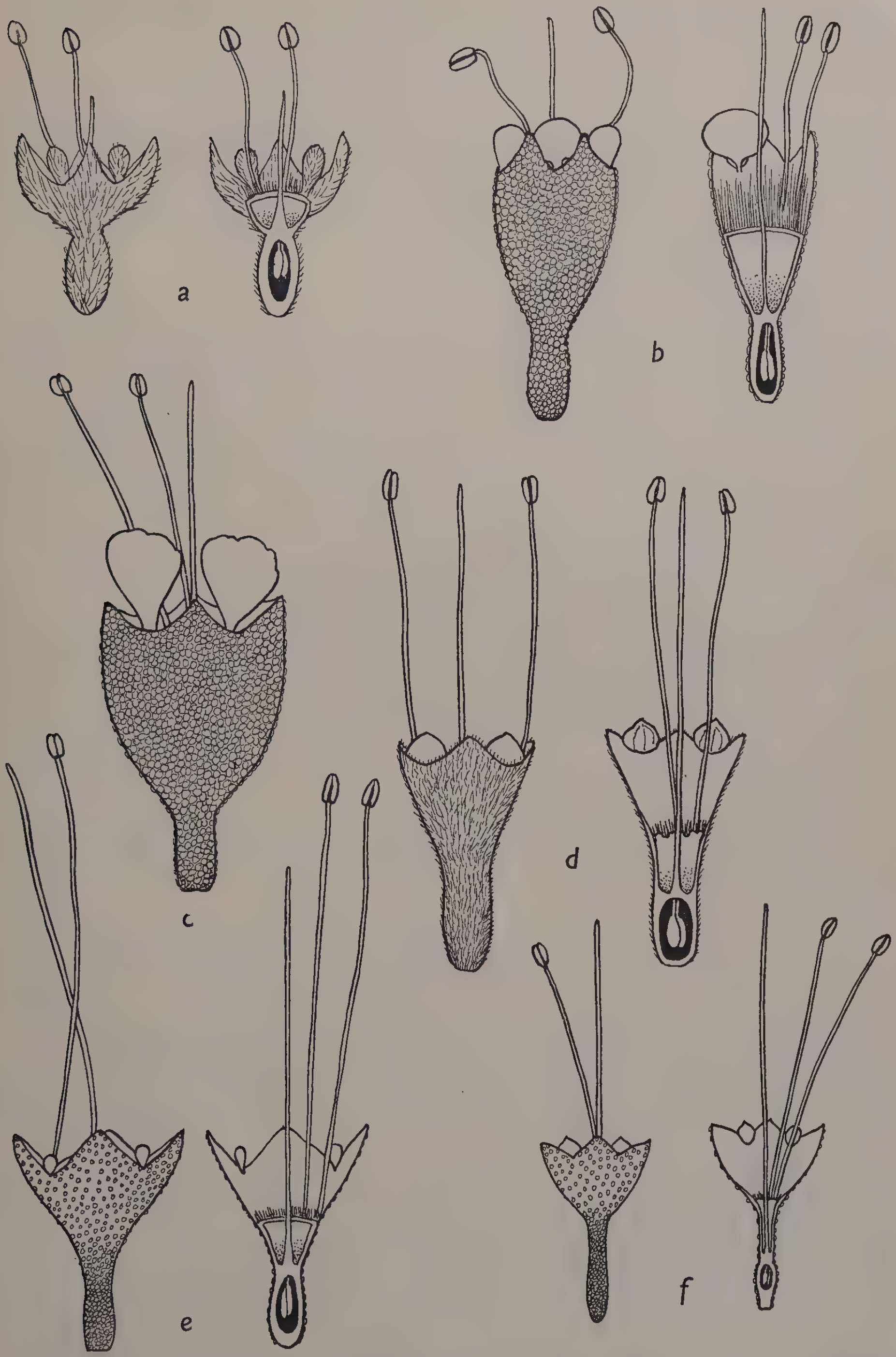

Fig. 2. Diagrams of flower structure. (*a–c*, × 5; *d–f*, × 2½.) (*a*) *Combretum hilarianum* D. Dietr. (*Riedel 862*); (*b*) *C. leprosum* Mart. (*Gardner 2161*); (*c*) *C. frangulifolium* Kunth (*Holt & Blake 826*); (*d*) *C. argenteum* Bertol. (*Hartweg 526*); (*e*) *C. farinosum* Kunth (*Hancock* s.n.); (*f*) *C. rohrii* Exell (*von Rohr 149*).

NICARAGUA. Chinandega: Realejo, *Ørsted 3417* (US). Nicaragua? 'San Carlos', *Barclay* s.n. (BM).

Vernacular names. Chupamiel (Salvador); Peine de Mico (Salvador).

11. Combretum farinosum Kunth, *Nov. Gen. & Sp. Pl.* vi: 110 (1823). Based on a plant found between Acapulco and Venta del Exido, Mexico. This is probably represented by *Bonpland 3894*, which may be taken as the type gathering. [Fig. 2*e*.]

Grislea secunda L., *Sp. Pl.* i: 348 (1753); non *Combretum secundum* Jacq.

Combretum polystachyum Pittier in *Contrib. U.S. Nat. Herb.* xviii: 243 (1917). Based on *Pittier 12140* from Nicaragua.

Distribution. Mexico to Costa Rica.

Specimens:

MEXICO. Chiapas: near Tuxtla Gutierrez, *Erlanson & Souviron 46* (BM). Sinaloa: Rosario, *Lamb 468* pro parte (US); *Montes & Salazar 118* (K; US); Mazatlan, *Ortega 118* (K), *5625* (US), *5676* (US); Imala, *Ortega 4180* (US); El Habal, *Ortega 5201* (US); Culiacan, *Ortega 6792* (US); Mazatlan, *Purpus 360* (US); S. Blas, *Rose, Standley & Russell 13107* (US); Mazatlan, *Rose, Standley & Russell 13849* (US); Rosario, *Rose, Standley & Russell 14510* (US); Mazatlan, *W. G. Wright 1226* (US). Tepic: Acaponeta, *Rose 1416* (US); Acaponeta, *Rose, Standley & Russell 14185* (US), *Rose 14185* (NY). Jalisco: *Diquet* s.n. (NY). Vera Cruz: Acasonica, *Galeotti 3051* (P); La Purga, *Greenman 234* (US); Cameron, *Purpus 8637* (BM); near Puerto Nacional, *Purpus 14002* (K), *14203* (BM). Colima: Manzanillo Bay, *Hinds* s.n. (K); Manzanillo, *Palmer 1067* (BM; K; US). Michoacan: Huetamo, Tacupa, *Hinton 5632* (BM, pro parte quoad spec. flor.); El Zapilote, *Nelson 6974* (US). Michoacan or Guerrero? 'Monte d'Inguaran', *Langlassé 9* (K; P; US), *10* (K; P; US). Guerrero: Acapulco, *Barclay 1994* (BM), s.n. (K); Acapulco, *Bonpland 3894* (PHB, type); Coyuca, *Hinton 5530* (K); Placeres, *Hinton 9977* (BM; K); Acapulco, *Palmer 397* (BM; K; US). Mexico: Temascaltepec, Guyayabal, *Hinton 3364* (K). Oaxaca: *Ghiesbreght 18* (P); S. Bartolo Yauhetepec, *Seler 1659* (K). Chiapas: S. Bartolome, *Goldman 764* (US). San Luis Potosi: La Solidad, near Potrero, *Hahn* s.n. (P); without precise locality (probably the same as the preceding specimen), *Hahn* s.n. (K). Mexico (unidentified localities): 'Antigua Paso Dna Juana', *Liebmann 3410* (US); 'Los Baños', *Heller 118* (PHD); without precise locality, *Jurgensen 174* (K); *Leybold 26* (US).

GUATEMALA. Guatemala: near Trapiche Grande, *Maxon & Hay 3420* (US). Jalapa: El Rancho, *Kellerman 5648* (US). Chiquimula: *Salas 646* (US). El Progresso: Barranquillo, *Popenoe 958* (US). Without precise locality, *Friedrichsthal* s.n. (K); *Skinner* s.n. (K).

HONDURAS. Valle: Tiger Island, Gulf of Fonseca, *Sinclair* s.n. (K).

SALVADOR. Sonsonate: Acajutla, *Hancock* s.n. (K); S. Antonio del Monte, *Standley 22144* (US). San Vicente: Tecoluca, *Shannon 5038* (K; US); S. Vicente, *Standley 21258* (US). San Miguel: Hacienda S. Antonio, *Calderón 2130* (US). La Union: La Union, *Standley 20652* (US).

NICARAGUA. Chinandega: Realejo, *Baker* s.n. (K; US); Realejo, *Sinclair* s.n. (K). Managua: Managua, *Chaves 172* (US). Granada: near Granada, *Levy 329* (P); *C. Wright* s.n. (US). Unidentified localities in Nicaragua: 'Boca Culebra', *Pittier 12013 pro parte* (US); 'Bords du Diquis à Curres', *Pittier 12140* (US).

COSTA RICA. Guanacaste: Gulf of Nicoya, *Hinds* s.n. (BM; K); Pigres, *Lankester K 62* (K).

Without locality or collector (BM, Hort. Cliff., type of *Grislea secunda*).

Vernacular names. Bejuco angarilla (Mexico); Carape (Mexico); Chupa-chupa (Salvador); Chupamiel (Salvador); Chupamiel de Peineta (Salvador); Papamiel (Costa Rica); Peineta (Guatemala, Salvador); Peinetella (Mexico, Nicaragua); Peinecillo (Mexico).

This species is comparatively uniform and usually easily distinguishable from the other species of the section by its silvery-greyish scales, which are rather larger than in the other species. The petals are usually small compared with those of *C. fruticosum* and do not nearly fill the spaces between the rather short, broad calyx-lobes. Pittier (in *Contrib. U.S. Nat. Herb.* xviii: 239–46 (1917)) has split up the species, mainly on the size and shape of the petals, but this does not appear satisfactory. Of the specimens cited above, *Rose, Standley & Russell 13849* is the most doubtful, the upper receptacle being much longer and narrower than in any other specimen here referred to *C. farinosum.*

12. **Combretum fruticosum** (Loefl.) Stuntz in *U.S. Dep. Agric. Bur. Pl. Ind. Seeds & Pl. Import.* no. 31: 86 (1914). Based on *Gaura fruticosa* Loefl. [Fig. 3*a–f*.]

Gaura fruticosa Loefl., *Iter Hispan.*: 248 (1758). Based on a plant collected by Loefling in Venezuela. No specimen has been found but the description agrees with this species which is, moreover, by far the most abundant in the region where Loefling collected.

Combretum occidentale L., *Syst. Nat.* ed. 10, ii: 999 (1759) nom. illegit. Based on *Gaura fruticosa* Loefl.

Combretum secundum Jacq., *Enum. Syst. Pl. Ins. Carib.*: 19 (1760); *Select. Stirp. Amer. Hist.*: 103, t. 176, fig. 30 (1763). Based on a plant growing at Carthagena, Colombia.

Combretum laxum sensu L., *Sp. Pl. ed.* 2, i: 496 (1762) pro parte quoad syn. *Gaura fruticosa* Loefl. This is often cited as *C. laxum* L. but was probably a misinterpretation of *C. laxum* Jacq. (1760). As Kölpin introduced the name into the German edition of Loefling's *Iter Hispanicum*, it is often wrongly cited as *C. laxum* Loefl.

Combretum formosum Don in *Trans. Linn. Soc. Lond.* xv: 420 (1827). Based on a specimen in Herb. Lambert collected near Rio de Janeiro.

Combretum oxypetalum Don, loc. cit. Based on a specimen in Herb. Lambert collected by Pavon in Guayaquil.

Combretum micropetalum DC., *Prodr.* iii: 19 (1825). Based on a specimen from Brazil.

? *Combretum tetragonum* Presl, *Reliq. Haenk.* ii: 25 (1836). Based on a plant from Mexico preserved in the Prague Herbarium (n.v.). If not this species it is probably *C. farinosum.*

Combretum aurantiacum Benth. in Hook., *J. of Bot.* ii: 222 (1840). Based on *Schomburgk 87* from Essequibo, British Guiana.

? *Combretum reticulatum* Presl ex Walp., *Rep. Bot. Syst.* ii: 65 (1843) nom. nud. Apparently a miscitation of *C. tetragonum* Presl.

Combretum loeflingii Eichl. in Mart., *Fl. Bras.* xiv, 2: 110 (1867) nom. illegit. Based on *Gaura fruticosa* Loefl. (erroneously cited as *C. laxum* Loefl.). Eichler was probably unaware of the name *G. fruticosa* in the original edition of Loefling's *Iter Hispanicum* and renamed '*C. laxum* Loefl.' because of the earlier *C. laxum* Jacq. (see note under *C. laxum* sensu L., above).

Combretum warszewiczianum Eichl., loc. cit. Based on specimens collected by Warszewicz in Costa Rica and Nicaragua.

Combretum benthamianum Heurck & Muell. Arg., *Obs. Bot.*: 220 (1870). Based on a specimen (now in Van Heurck's Herbarium, Antwerp) collected by Barclay in the Gulf of Fonseca, Honduras.

Combretum gloriosum Rusby in *Mem. Torrey Bot. Cl.* vi: 35 (1896). Based on *Bang 1427* from Guanai-Tipuani, Bolivia.

? *Combretum lindbergii* Eichl. ex Rusby, loc. cit. nom. nud. This is probably an error for *C. loeflingii* Eichl.

Combretum farinosum var. *phaenopetalum* J. D. Sm. in *Bot. Gaz.* xxiii: 7 (1897). Based on *Nelson 3534* from Huehuetenango, Guatemala.

Combretum superbum Pittier in *Contrib. U.S. Nat. Herb.* xviii: 242 (1917). Based on *Pittier 2158* from near Culebra, Panama.

Combretum phaenopetalum (J. D. Sm.) Pittier, tom. cit.: 243 (1917). Based on *C. farinosum* var. *phaenopetalum.*

Combretum lepidopetalum Pittier, tom. cit.: 245 (1917). Based on *Pittier 5006* from Coclé, Panama.

Combretum multidiscum Rusby, *Descr. New Sp. S. Amer. Pl.*: 69 (1920). Based on *H. H. Smith 874* from S. Marta, Colombia.

? *Combretum trinitense* Britton in *Bull. Torrey Bot. Cl.* xlviii: 334 (1922). Based on *Britton, Freeman & Watts 2699* from Trinidad. The specimen is in fruit and cannot be determined with certainty but it probably belongs to this species.

Combretum fruticosum (Loefl.) Fawc. & Rendle in *J. of Bot.* lxiii: 115 (1925). Based on *Gaura fruticosa* Loefl. Antedated by *Combretum fruticosum* (Loefl.) Stuntz (1914).

Combretum loeflingii subsp. *ornithophilum* Suessenguth in *Mitteil. Bot. Staatssamml. Münch.* i: 14 (1950). Based on *Vogl 1447* from Maracay, Venezuela.

Distribution. Widespread from Mexico to Argentina.

Specimens:

MEXICO. Sinaloa: *Ortega 4718* (US). Jalisca: near S. Blas, Nayarit, *Ferris 5530* (US); south of Puerto Vallarta, *Mexia 1130* (BM). Hidalgo: near Taxmalac, *Ule 4254* (US). Vera Cruz: S. Lucrecia, *Mell 672* (US). Guerrero: above Igula, *Pringle 8371* (BM; Ley; K; US); near Iguala, *Rose, Painter & Rose 9414* (US); Balsas, *Lemmon 158* (K). Guerrero or Michoacan: El Calabazal, *Langlassé 461* (K; US). Michoacan: Huetamo, Tacupa, *Hinton 5632* (BM pro parte quoad spec. fruct.). Mexico: Temascaltepec, *Hinton 728* (K). Oaxaca: Fepenixtlalmaca, *Conzatti 4378* (US); between Pinotepa and Jamiltepec, *Nelson 2349* (US). Tabasco: between S. Juana Bautista and Atasta, *Rovirosa 137* (K). Campeche: Apazote, *Goldman 517* (US). Yucatan: Mokel, *Ule 4940* (US).

BRITISH HONDURAS. R. Sarstoon, *Campbell 70* (K); El Cayo District, Yucatan, *Gentle 2388* (K); Orange Walk, *Moloney 36* (K); Vaca Falls District, *Record* s.n. (US); Mullins River road, *Schipp 36* (BM; K; US); Big Creek, *Schipp 42* (BM; K; US). Without precise locality: *Kinloch 34* (BM); *Peck 344* (K); *Smart AXXXI* (BM).

GUATEMALA. El Peten: La Libertad, *Lundell 2433* (BM). Huehuetenango: near Neuton, *Nelson 3534* (US, type of *C. farinosum* var. *phaenopetalum*). Izabal: Puerto Barrios, *Deam* s.n. (US); near Quirigua, *Standley 24034* (US). Alta Verapaz: Cubilquitz, *von Tuerckheim 7621* (K; US); *7862* (US). Baja, Vera Paz or Chiquimula: *Watson 290* (US). Santa Rosa: *Heyde & Lux 4173* (BM; K; US). 'Inter Granados et Tortuga', *Bernoulli & Cario 2979* (K).

HONDURAS. Gulf of Fonseca, *Barclay* s.n. (VH, type of *C. benthamianum*). Without precise locality (probably the same gathering as the preceding specimen), *Barclay* s.n. (K).

NICARAGUA. Chontales: *Tate 63(250)* (K), *64(256)* (BM; K). 'Sangsangta District', *Schramm 5* (US).

SALVADOR. San Salvador: near S. Salvador, *Renson 68* (NY; US); near S. Salvador, *Warszewicz* s.n. (US, fragment). La Unión: near La Unión, *Standley 20823* (US). Without precise locality, *Renson 36* (US).

COSTA RICA. R. Ceibo, near Buenos Aires, *Tonduz 6704* (BM; US).

PANAMA. Coclé: between Aguadulce and R. Chico, *Pittier 5006* (US, type of *C. lepidopetalum*); near Penonome, *Williams 72* (NY; US). Canal Zone: near Cristobal, Colon, *Broadway 162* (US), *589* (US); near Salamanca Hydrographic Station, R. Pequeni, alt. 70–80 m.; *Dodge, Steyermark & Allen 17981* (BM); R. Grande, *Hayes 466* (K); Punta Paitillo, *Heriberto 214* (US); between Empire and Mandinga, *Piper 5489*; near Culebra, *Pittier 2158* (US, type of *C. superbum*); near Port Sherman, *Standley 31016* (US). Panama: near Panama, *Hayes 783* (NY); near Panama, *Sargent 10* (US); Bella Vista, *Standley 25308* (US); Corozal Road, near Panama, *Standley 28081* (US). 'Sabanas',

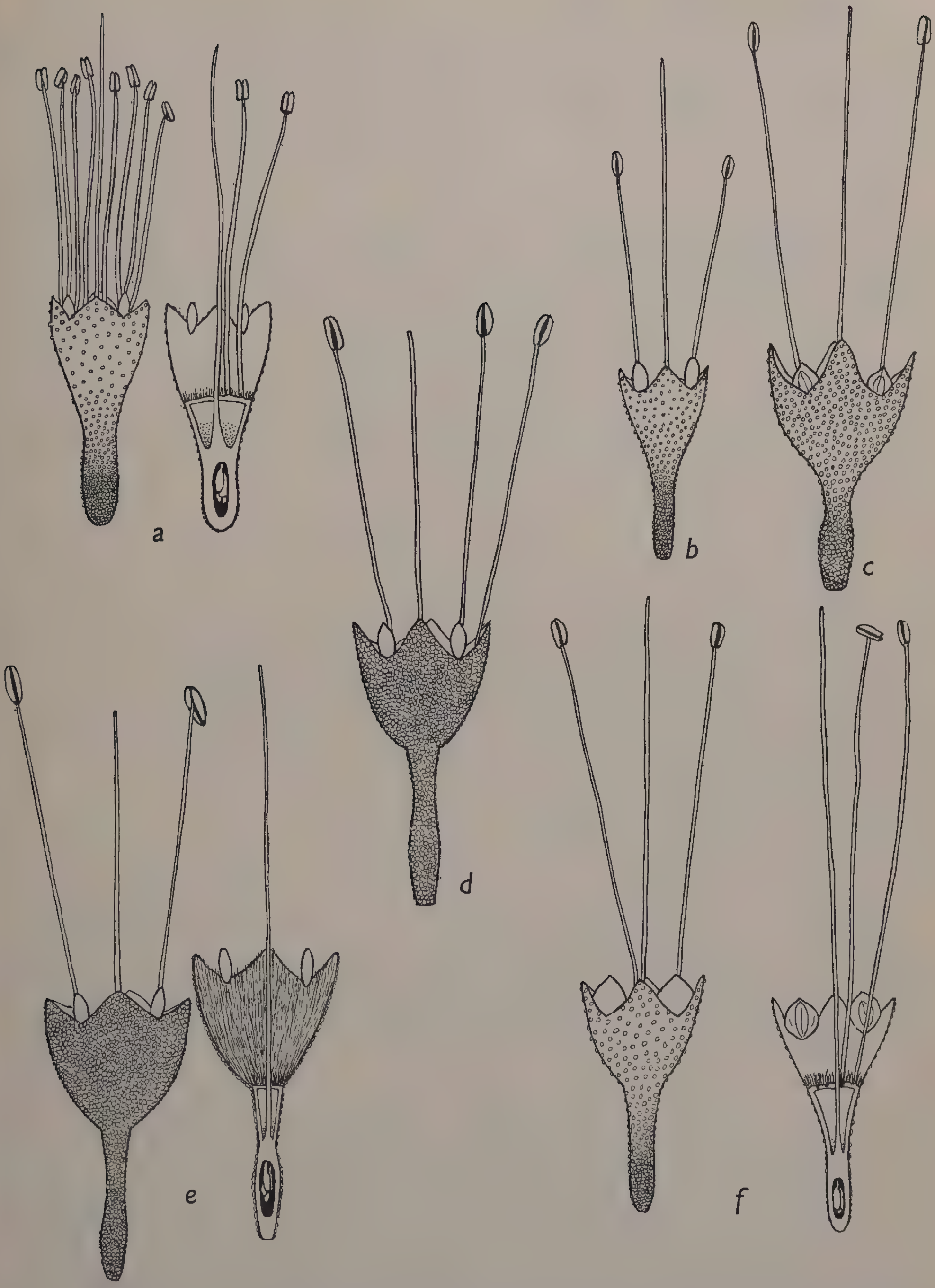

Fig. 3. Diagrams of flower structure showing variation in *Combretum fruticosum* (Loefl.) Stuntz. (×2½.) (*a*) *Hassler 5881*; (*b*) *Heyde & Lux 4143*; (*c*) *Schomburgk 87*; (*d*) *Pringle 8371*; (*e*) *Blanchet 29*; (*f*) *Rovirosa 137*.

Killip 3295 (US). Without precise locality: *Duchassaing* s.n. (P), *Halsted* s.n. (NY), *Hayes 308* (NY), *Seemann* s.n. (BM).

WEST INDIES. Trinidad: Chacachacare, *Britton, Freeman & Watts 2699* (K; US); Caura Valley Road, *Britton & Mendelson 1586* (US); Blanchisseuse Road, near 3-mile post, *Broadway 6001* (BM; K; US); Claxton Bay, *Broadway 7857* (K); Chacachacare, *Broadway 10329* (K); *Crueger* s.n. (K); *Fendler 282* (BM; K); *Lockhart* s.n. (K); *Riedlé 38* (PHJ); *von Rohr 43* (BM); *Botanic Gardens Herbarium 1095* (US), *2054* (US), Union Bay, *3582* (US).

COLOMBIA. S. Marta, *Bertero 35* (P); near Viota, *Dawe 76* (K; US); *Herb. Desvaux* s.n. (P); Caracolicito, *Dugaud & Garcia 2498* (BM); near Baranquilla, *Elias 393* (US), *609* (US), *1350* (BM; K), *1354* (K); melgar, R. Magdalena, *Goudot 1* (P); Coyayma, *Goudot* s.n. (P); between La Jagua and Becerrel, *Haught 2275* (BM); Cartagena, *Heriberto 256* (NY); Opia, *Holton 924* (K; NY); Bolivar, near Turbaco, *Killip & Smith 14209* (BM; NY; US); Tolima, *Lehmann 2621* (K; US); R. Haitia, *Linden 1639* (BM; K; P). Without precise locality, *Mutis 1860* (US), *3476* (US), *3805* (US); Bolivar, Buenavista, *Pennell 4018* (NY; US); Bolivar, Cienaga de Oro, *Pennell 4138* (NY); Cundinamarca, *Perez 524* (US); S. Marta, *Purdie* s.n. (K); S. Marta, *Richard* s.n. (P); Ocana, Aguachica, *Schlim 279* (K; P); *H. H. Smith 874* (BM; K; P; US, type of *C. multidiscum*); Fequendama, *Triana 6087* (BM); Bogota and Mariquisa, *Triana* s.n. (K; P); S. Marta, without collector (VH).

VENEZUELA. Zulia: near Mene Grande, *Pittier 10652* (NY; US); near Perijá, *Tejera 46* (US). Trujillo: between Quebrada Seca bridge and R. Matatán, *Pittier 13304* (NY; US). Yaracuy: Los Cañizos, *Pittier 8761* (US). Carabobo: near Las Trincheras, near Valencia, *Pittier 7659* (US); valley of Vijirima, near Guacara, *Pittier 8168* (US); near Valencia, *Pittier 8726* (US); Valencia, *Rose 21836* (US). Aragua: S. Juan de los Morros, *Pittier 10161* (NY; US); Maracay, *Vogl 1447* (Mu, type of *C. loeflingii* subsp. *ornithophilum*). Caracas: *Funcke 310* (P). Anzoategui: near Barcelona, *Chafer* s.n. (P); near R. Pao, *Pittier 14545* (BM). Miranda: near Petare, *Pittier 9901* (US); Monagas: R. Tigre, *Moritz 1983* (BM; P; PHD; US). Merida: near Tovar, *Fendler 395* (K; NY). Portugesa: near Aparición, *Pittier 12084* (NY; US). 'El Hacha', *Brown 201* (K), s.n. (K). Without precise locality, *Funcke 531* (BM; K).

BRITISH GUIANA. *Jenman 6946* (K; NY); Essequibo, *Schomburgk 87* (BM; K, type of *C. aurantiacum*; P); R. Rupununi *A. C. Smith 2377* (K); Kanuka Mts., *A. C. Smith 3105* (K).

BRAZIL. Amazonas: S. Marcos, *Ule 7859* (K); R. Acre, *Ule 9664* (K). Pará: Ilheos, *Moricand* s.n. (K). Piauhy: Oeiras, *Gardner 2466* (BM; K). Ceará: coastal region, *Bolland 11* (K); Crato, *Gardner 1948* (BM; K). Pernambuco: Tapera, *Pickel 2750* (BM). Matto Grosso: *Leeson* s.n. (BM, coll. carp.); Guia, near Cuyabá, *Malme 1630* (US). Goyaz: *Burchell 7220* (K; P), *7288–3* (K); *St-Hilaire 735* (P). Bahia: *Blanchet 29* (BM; P). Minas Geraes: *Clausen 72* (P); *Gardner* s.n. (BM); Fazenda S. Terezinha, Huitaba, *Macedo 779* (BM); Rio do Peixe, *Regnell* s.n. (P); *St-Hilaire 1325* (P); Lagoa Santa, *Warming* s.n. (P). São Paulo: *Bowie & Cunningham 422* (BM); *St-Hilaire 754* (P). Rio de Janeiro: *Herb. Gay* s.n. (K); Gavea, *Glaziou 3949* (K; P; US); Petropolis, *Glaziou 8337* (K; P), *10727* (K), *12659* (K; P; US), *13805* (K; P); *Graham* s.n. (K); Monte Telegráphico, *Martius 92* (BM; K; P; PHD; VH); *St-Hilaire 62* (P); *Vauthier 45* (PHD), *166* (P); *Weddell 165* (P), *452* (P); Belem, *Weir 29* (BM; K). Paraná: Therezina, *Dusen 11220* (K), *11221* (K); Alexandra, *Dusen 15475* (Ley; K); North Paraná, *Tessmann 6027* (K). S. Catharina: Tubarão, *Ule 1089* (US), s.n. (P). Rio Grande do Sul: *Gaudichaud 1297* (P); *Isabelle* s.n. (P). Unidentified localities: 'Near Moijm', *Bowie & Cunningham* s.n. (BM); 'Maynas', *Poeppig 1898* (P). Without locality: *Blanchet 1549* (BM); *Lalande* s.n. (P); *Luschnath* s.n. (K; P; PHD); *Pringle 8371* (P); *Riedel 530* (BM; Ley; K, pro parte; P; US), *2050* (Ley); *2050, 1759* (P); *St-Hilaire* s.n. (P); *Sello* s.n. (BM, fragment); *Vauthier* s.n. (P).

ECUADOR. Without precise locality, *Pavon* s.n. (BM, type of *C. oxypetalum*?).[1]

PERU. LORETO: lower R. Huallaga, *Killip & Smith 29014* (BM); Cachipuerte, *Klug 3130* (K). SAN MARTIN: R. Cainarachi, *Klug 2608* (BM; K); Chazuta, *Klug 4118* (BM; K); Juan Jui, *Klug 4325* (BM; K); Tarapoto, *Spruce 3969* (BM; K; P; VH). JUNIN: La Merced, *Killip & Smith 23457* (BM), *23740* (BM); Puerto Bermudez, *Killip & Smith 26470* (BM). Without precise locality: *Gay* s.n. (P); *Ruiz* s.n. (BM).

BOLIVIA. Guanai-Tipuani, *Bang 1427* (BM; K; US). Without precise locality, *White 951* (K).

PARAGUAY. Picada de Sapucai, *Balansa 2336* (BM; K); between R. Apa and R. Aquidaban, *Fiebrig 5018* (BM; Ley; K); R. Alto Paraná, *Fiebrig 5854* (BM; K; US), *5938* (BM; Ley; K; US); near Sapucay, *Hassler 1664* (BM; K; P; PHD); Sierra de Maracayú, *Hassler 5581* (BM; K; P); R. Capibary, *Hassler 5925* (K; P); Upper R. Yaca, *Hassler 6750* (BM; K; P); Upper R. Apa, *Hassler 8360* (BM; K; P); Cordillera de Villa-Rica, *Hassler 8858* (BM); Central Paraguay, *Morong* s.n. (US).

URUGUAY. R. Uruguay, *Rosengurtt B1066* (BM).

ARGENTINA. MISIONES: S. Ignacio, *Quiroga* s.n. (BM); S. Ana, *Rodriguez 316* (BM), *316a* (BM); Posadas, *Van de Venne* s.n. (BM); Posadas, *Vattuone & Bianchi 88* (US); Nacauguazú, *Vattuone & Bianchi 172* (US). CORRIENTES: S. Tomé, *Venturi* s.n. (BM). ENTRE RIOS: R. Uruguay, Salto Grande, *Castellaños* s.n. (BM); Gualeguaychu, *Jurado* s.n. (BM); Concepción del Uruguay, *Lorentz* s.n. (BM; K; US); Puerto Yerua, *Pennington* s.n. (BM); *Swartz* s.n. (K).

Vernacular names. Bejuco melero (Venezuela); Escobetilla (Mexico); Mata de miel (Venezuela).

As here delimited, this widespread species shows considerable variation in the size of the flowers, shape and size of the petals, shape and indumentum of the upper receptacle, and shape and indumentum of the leaves. Although the species, in its present circumscription, appears heterogeneous, the variations mentioned show no correlation with each other or with geographical distribution. To divide it into a number of 'species' or taxa of lower rank, in our present state of knowledge, would not serve any useful purpose. Some of the specimens cited above approach *C. argenteum* and others approach *C. farinosum*. In fact the members of this section form a 'complex' of closely related species and the system proposed is largely one of convenience. I have separated as species those groups of individuals that seem sufficiently distinct for herbarium identification, and left the great mass of material under the name *C. fruticosum*. Field-work, combined with genetical studies, will no doubt eventually produce a much more accurate classification. Fig. 3 shows the more extreme variations and these, indeed, appear very different, but future workers should beware of separating a number of microspecies without studying the large amount of material which I have been able to see, for otherwise it is impossible to realize the extent to which the extreme forms are linked by intermediates.

13. **Combretum rotundifolium** Rich. in *Act. Soc. Hist. Nat. Par.* i: 108 (1792). Based on a specimen collected by Le Blond in Cayenne.

Combretum laxum sensu Aubl., *Pl. Guian.* i: 351, t. 137 (1775), pro parte excl. syn.; non *C. laxum* Jacq. (1760).

Combretum elegans Kunth, *Nov. Gen. & Sp. Pl.* vi: 109 (1823). Based on a plant growing on the banks of the R. Orinoco, near La Playa de Guaripa.

Combretum secundum sensu Don in *Trans. Linn. Soc. Lond.* xv: 419 (1827), pro parte quoad syn. *C. elegans* et *C. laxum* et specim. cit.

Combretum Aubletii DC., *Prodr.* iii: 19 (1828). Based on '*C. laxum* Aubl.' (see above).

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[1] This is probably the specimen described by Don as *C. oxypetalum* but there is no mention on the sheet of the locality 'Guayaquil' cited by him.

Combretum magnificum Mart. in *Flora*, xxiv, Beibl. 2: 4 (1841). Based on plants growing at Goajura and elsewhere in the states of Pará and R. Negro, Brazil.

Combretum guianense Miq. in *Ann. Mag. Nat. Hist.* xi: 12 (1843). Based on *Focke 407* from near Bergendaal, Surinam.

Combretum punctatum Steud. in *Flora*, xxvi, 2: 761 (1843); non *C. punctatum* Bl. (1825). Based on *Hostmann & Kappler 825* from Surinam.

Distribution. From Colombia to Cayenne, Brazil, Peru and Bolivia.

Specimens:

COLOMBIA. Vaupes: R. Macaya, *Schultes 5501* (n.v.).

VENEZUELA. Orinoco, Playa de Guaripa, *Bonpland 840* (P); Brazo Casiquare, *Holt & Blake 658* (BM); Lower Orinoco, *Purdie* s.n. (K); Lower Orinoco, Manoa, *Rusby & Squires 265* (US); Casiquare, *Spruce* s.n. (K).

BRITISH GUIANA. R. Cuyuni, *Aitken 1068* (K); below Mt. Everard, R. Barima, *Anderson 237* (K); R. Mazaruni, *Appun 274* (K); R. Oronoque, *Beddington 10* (K); Upper R. Rupununi, *De la Cruz 1374* (NY; US); Mazaruni Station, *Forest Dep. 3998* (K); R. Essequibo, *Forest Dep. 4087* (K); junction of R. Mazaruni and R. Cuyuni, *Graham 174* (US); R. Corentyne, *Jenman 475* (P); R. Mazaruni, *Jenman 737* (K); R. Demerara, *Jenman 5046* (NY); R. Cuyuni, *Martyn 259* (K); Upper Essequibo, *Myers 5705* (K); R. Demerara, *Parker* s.n. (K); R. Rupununi, Isherton, *A. C. Smith 2493* (K); R. Cuyuni, *Sandwith 628* (K); R. Corentyne, *im Thurn* s.n. (K); R. Cuyuni, Crab Fell, *Tutin 15* (K). Without precise locality, *Pollard 58* (K).

SURINAM. Upper R. Coppename, *Boon 1251* (Ut); R. Wajombo, *Boschwezen 1027* (Ut); R. Gonini, *Boschwezen 3689* (Ut); Bergendaal, *Focke 407* (type of *C. guianense*; Ley); Pará District, *Hostmann & Kappler 825* (Type of *C. punctatum*; BM; Caen; K; P; PHD; Ut); R. Lucie, *Hulk 353* (Ut); R. Marowyne, *Kappler 1998* (P; Ut); Cassipoera Creek, *Kegel 1192* (Go; Ut); R. Coppename, near Kaaimanstone, *Lanjouw 701* (BM; K; Ut); R. Coppename, *Lanjouw 1158* (BM; Ut); Suriname, *Nolte* s.n. (Go); R. Kabalebo, Avanavero Falls, *Pulle 442* (Ut); R. Suriname, *Tresling 2* (Ut); Upper R. Suriname, *Tresling 275* (Ut); R. Gonini, *Versteeg 156* (Ut); R. Tapanahoni, *Versteeg 707* (Ut); Upper R. Suriname, *Wullschlaegel 151* (Br). Without precise locality: *Hostmann* s.n. (Ley); *Kickx* s.n. (Caen); *Splitgerber 112* (Ley), *829* (Ley).

CAYENNE. Upper Maroni, *Crevaux* s.n. (P); La Mana, *Leschenault*, s.n. (P); Maroni, *Mélinon 297* (P); La Mana, *Mélinon* s.n. (P); La Mana, *Sagot 849* (BM; Caen; K; PHD), s.n. (P). Without precise locality: *Aublet* s.n. (BM); *Le Blond* s.n. (PHL); *Perrottet* s.n. (P); *Richard* s.n. (P, type).

BRAZIL. Amazonas: R. Solimões, *Spruce 1646* pro parte (K; PHD). Pará: *Burchell 10052* (K; P); *Glaziou 9791* (BM, fragment; Cop; P); R. Arapecuru, *Spruce 541* (K; PHD), s.n. (K). Matto Grosso: near Tabajara, Upper R. Machado, *Krukoff 1429* (K).

PERU. Loreto: Pampa del Sacramento, *de Castelnau* s.n. (P); Encanto, *Fox 97* (K), *113* (K).

BOLIVIA. R. Beni, *Rusby 1773* (NY).

14. Combretum rohrii Exell, sp.nov. [Fig. 2*f*] *Frutex?*, ramulis fere glabris nonnunquam ± quadrangularibus. *Folia* opposita petiolata, petiolo 4–6 mm. longo, lamina elliptica late elliptica vel ovato-elliptica, ad 8 × 5 cm., subcoriacea supra glabra nitidula subtus atro-ferrugineo-lepidota, lepidibus conspicuis margine vix contiguis, apice acuminata vel acuta basi acuminata vel cuneata, costis lateralibus utrinsecus 5–6. *Flores* tetrameri (vel nonnunquam pentameri) subsessiles vel breviter pedicellati in spicas axillares dispositi. *Receptaculum* superius apicem versus campanulatum, 6 × 4·5 mm., basin versus angustissime infundibuliforme, 2·5 × 1 mm., dense rufo-lepidotum ceteroqui glabrum, inferius fusiforme, 2·5 × 1 mm., dense rufo-lepidotum ceteroqui glabrum. *Lobi calycis* deltoidei, 1·5 × 2 mm. *Discus* angustissime infundibuliformis, 3 × 1 mm., margine liber (*c.* 0·5 mm.), sparse pilosulus. *Petala* rotundata apice acuminata, 2 × 2 mm., glabra. *Stamina* 8, exserta, 1·5 cm. longa. *Stylus* exsertus, 2 cm. longus, glaber. *Fructus* suborbicularis vel pyriformis 4-alatus, alis tenuibus, rufolepidotus, ad 2 × 1·7 cm.

DISTRIBUTION. Cayenne.

SPECIMENS:

CAYENNE. *Le Blond* s.n. (BM, fragment; P); *Perrottet* s.n. (P); *Richard* s.n. (BM, fragment; P); *von Rohr 149* (BM, type).

The affinity is with *C. rotundifolium* and *C. assimile*, from both of which it differs by the much smaller flowers and small, sub-coriaceous leaves. The species is as yet insufficiently known.

15. **Combretum assimile** Eichl. in Mart., *Fl. Bras.* xiv, 2: 109 (1867). Based on *Spruce 1523* from Amazonas, Brazil.

DISTRIBUTION. Brazil and Peru.

SPECIMENS:

BRAZIL. AMAZONAS: mouth of R. Solimões, *Spruce 1523* (type; BM; K; P; PHD). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 11945* (K). Without precise locality: *Sello* s.n. (BM).

PERU. LORETO: Fortaleza, near Yurimaguas, alt. *c.* 140 m., *Klug 2785* (BM; K).

According to Klug this is a vine with yellowish-green and red flowers. This species is still insufficiently known and its relationship with *C. guanaiense* remains uncertain.

16. **Combretum sambuense** Pittier in *Contrib. U.S. Nat. Herb.* xviii: 242 (1917). Based on *Pittier 5548* from southern Darien, Panama.

DISTRIBUTION. Panama, Colombia and Peru.

SPECIMENS:

PANAMA. R. Sambu, southern Darien, *Pittier 5548* (US, type).

COLUMBIA. ANTIOQUIA: Puerto Berrio, *Pennell 3772* (NY).

PERU. LORETO: R. Pachitea, between Puerto Victoria and Puerto Leguia, *Killip & Smith 26826* (BM; US).

17. **Combretum guanaiense** Rusby in *Mem. Torrey Bot. Cl.* vi: 34 (1896). Based on *Bang 1320* from La Paz, Bolivia.

DISTRIBUTION. Brazil, Peru and Bolivia.

SPECIMENS:

BRAZIL. MINAS GERAES: Petropolis, *Glaziou 10727* (K; P).

PERU. LORETO: R. Acre, Seringal, Auristella, *Ule 9663* (Ley; K).

BOLIVIA. LA PAZ: Guanai, *Rusby 623* (BM; K; NY; US); Guanai-Tipuani, *Bang 1320* (BM; K; US, type). SANTA CRUZ: Buenavista, *Steinbach 7144* (BM; K).

Ule 9663 is said to be from Peru on the Kew ticket. This species may eventually prove to be the same as *C. assimile*.

18. **Combretum bassleranum** Mildbr. in *Notizbl. Bot. Gart. Berl.-Dahl.* ix: 143 (1924). Based on *Tessmann 3208* from Loreto, Peru.

DISTRIBUTION. Peru.

SPECIMENS:

PERU. LORETO: Yarina Cocha, *Tessmann 3208* (Type; BM, fragment).

19. **Combretum lanceolatum** Pohl ex Eichl. in Mart., *Fl. Bras.* xiv, 2: 110 (1867). Based on plants collected by Pohl in the province of Goyaz and near R. Maranhão. [Fig. 4*a*.]

Combretum glaziovianum Taub. ex Glaziou, in *Bull. Soc. Bot. Fr.* liv, *Mém. 3*: 204 (1908) nom. nud. Based on *Glaziou 10715* from near Campos, Rio de Janeiro, Brazil.

DISTRIBUTION. Brazil and Paraguay.

SPECIMENS:

BRAZIL. PARÁ: S. João de Araguaya, *Burchell 8868* (K; P); near Cassipa, R. Tapajos, *Krukoff 1239* (B; K). CEARA: S. Cruz, *Dahlgren* s.n. (K); *Gardner 1594* (BM; K; P). ALAGOAS: Paulo Affonso Falls, *Chase 7807* (US). MATTO GROSSO: *D. Smith 144* (K). GOYAZ: between Cavalcanti and Conceição, *Burchell 7964* (K). BAHIA: *Page* s.n. (NY). RIO DE JANEIRO: Lagoa do Cambello, near Campos, *Glaziou 10715* (K; P, type of *C. glaziovianum*). Without precise locality: *Pohl* s.n. (BM, part of type collection?); *Riedel 24* pro parte (P), s.n. (US).

PARAGUAY. Near Concepción, *Hassler 7181* (BM; K; P).

Vernacular name. Mofumbo (Brazil).

20. Combretum llewelynii Macbr. in *Field Mus. Publ. Bot. Ser.*, xi: 31 (1931). Based on *Williams 143* from Loreto, Peru.

DISTRIBUTION. Peru.

SPECIMENS:

PERU. LORETO: R. Itaya, *Williams 143* (Type; BM; fragment).

The type is in the herbarium of the Chicago Natural History Museum. Examination of two flowers, kindly sent by the Deputy Director, shows that this species differs very strikingly from all the other described species of the section by its elongated-triangular sharply pointed calyx-lobes. It seems, however, to be correctly placed in Sect. *Eucombretum.*

8. Sect. CACOUCIA (Aubl.) Engl. & Diels

21. Combretum cacoucia Exell apud Sandwith in *Bull. Misc. Inf. Kew,* 1931: 469 (1931). Based on *Cacoucia coccinea* Aubl. [Fig. 4*b*.]

Cacoucia coccinea Aubl., *Pl. Guian.* i: 450, t. 179 (1775). Based on a plant collected by Aublet 'ad ripam fluvii Sinemariensis'.

Schousboea coccinea (Aubl.) Willd., in L., *Sp. Pl.* ed. 4, ii: 578 (1779). Based on *Cacoucia coccinea* Aubl.

Terminalia cacoucia Baill., *Hist. Pl.* vi: 275 (1877) nom. illegit. Based on *Cacoucia coccinea* Aubl. This is illegitimate because the epithet '*coccinea*' should have been used.

Combretum coccineum (Aubl.) Engl. & Diels in Engl., *Mon. Afr. Pflanz.-Fam. & -Gatt.* iii: 110 (1899) nom. illegit.; non *C. coccineum* (Sonner.) Lam. (1785).

Combretum constrictum sensu Roberty in *Candoll.* xi: 90 (1947–8) pro parte quoad syn. *C. cacoucia*; non *C. constrictum* (Benth.) Laws. (1871).

DISTRIBUTION. British Honduras to Brazil.

SPECIMENS:

BRITISH HONDURAS. Yucatan, Stann Creek, *Gentle 1881* (K), *2700* (K), *2753* (K); *Robertson 222* (BM); *Schipp 87* (BM; K; US).

GUATEMALA. YZABAL: R. Chacon, *Johnson 1236* (BM); Yzabal, *J. D. Smith 1646* (K; P; US). 'Entre Rios', *Kuylen* s.n. (K); 'Eastern portions of Vera Paz and Chiquimula', *Watson 322* (US).

HONDURAS. ATLANTIDA: Lancetilla Valley, *Standley 56581* (US); Tela, *Standley 56586* (US); Tela, *Van Severen 43* (US); R. Esperanza, Puerto Siena, *Wilson 89* (US); R. Salado, *Yuncker, Koepper & Wagner 8331* (BM); 'Cuyamel', *Carleton 481* (US).

NICARAGUA. S. JUAN DEL NORTE: near Greytown, *C. L. Smith 11* (US).

PANAMA. CANAL ZONE: Gatun, *Hayes 8* (K; US), s.n. (US); Lion Hill Station, *Hayes 541* (BM; K); Gatun, *Heriberto 110* (US); R. Chagres, below Gatun, *Maxon 4798* (US); Frijoles, *Pittier 2692* (US). COLON: Camp Pina, *Allen 3432* (BM); R. Culebra, above S. Isabel, *Pittier 4169* (US).

WEST INDIES. TRINIDAD (fide Williams, *Fl. Trin. & Tob.* i, 5: 332 (1932), no specimen seen).

VENEZUELA? Without precise locality, *Bonpland* s.n. (PHB).

BRITISH GUIANA. R. Mazaruni, *Appun 288* (K); R. Koriabo, *Archer 2373* (K); Mazaruni Station, *Forestry Dep. 3572* (K); *Hancock* s.n. (K); R. Corentyne, *Jenman 355* (K); R. Mazaruni, *Jenman 763* (K), *5333* (BM); R. Essequibo, *Jenman 1326* (K); R. Demerara, *Jenman 4890* (BM); Moraballi Creek, near Bartica, R. Essequibo, *Sandwith 619* (K); *Schomburgk 33* (P), *272* (BM; K); Roraima, *Schomburgk 758* (K; P); R. Corentyne, *im Thurn* s.n. (K). Without precise locality, *Anderson* s.n. (BM).

SURINAM. Upper R. Coppename, *Boon 1257* (Ut); R. Corentyne, Apoera Is., *Boschwezen 2035* (Ut); Wahamiri Forest Reserve, *Boschwezen 3343* (Ut); Upper R. Cottica, *Focke 23* (Ley); Cassipoera Creek, *Kegel 1191* (Go); 70 km. along the railway, *Maguire 23623* (K); Middle R. Nickerie, *Tulleken 409* (Ley); R. Tapanahoni, *Versteeg 540* (Ut); Lower R. Coppename, *Went 126* (Ut); Upper R. Suriname, *Wullschlaegel 152* (Br; Go); R. Suriname, *Wullschlaegel* s.n. (Br). Without precise locality: *Focke* s.n. (P); *Hostmann 1032* (BM; Caen; K; P); *Splitgerber 109* (Ley), *334* (Ley).

CAYENNE. Ouanary, *Geay 1903* (P), *1904* (P), *1905* (P); St Laurent du Maroni, *le Moult 9* (P); Rives de Kau, *Mélinon 296* (P); Maroni, *Mélinon 308* (P), *381* (BM; K; P); Acarouany, *Sagot 242* (BM; Caen; Go; K; P); Ile Portal Bar, *Sagot*, s.n. (P); Godebert, *Wachenheim 52* (BM; K; P). Without precise locality: *Aublet* s.n. (BM, type); *Herb. Lamarck*, without collector (PHL); *Leprieur* s.n. (P); *Martin 110* (BM), s.n. (BM); *Mélinon 45* (P), *69* (P), *444* (P), s.n. (P); *Poiteau* s.n. (K); *Richard* s.n. (P).

When Roberty (in *Candoll.* xi, 91–2 (1947–8)) quotes me, beginning '*Combretum Cacoucia* is undoubtedly closely allied to *C. Mooreanum* Exell from West Africa' and ending 'There is every gradation of relationship through such species as *C. dolichopetalum* Engl. & Diels and *C. grandiflorum* G. Don to what may be considered typical *Combretum* species' this might appear, out of its context, to support his remarkable conception of *C. constrictum*, but the gradation referred to is between the genera *Cacoucia* and *Combretum* and was intended to show that these cannot be satisfactorily generically separated. Roberty (op. cit. 92) also comments on wingless fruits in *Combretum* saying: 'Nous ne reviendrons pas ici sur le caractère fallacieux des fruits désailés, qui sont de simples aberrations stériles et pathogénètes communes aussi bien dans les *Combretum* que dans les *Terminalia*.' It is true that sterile, wingless fruits are often produced in winged-fruited species of *Combretum* by galling, but there are many species that always have ridged or angled fruits which are quite normal and fertile. These are generally supposed to be water-borne. *Combretum cacoucia* has fruits of this kind and has never been found with winged fruits to my knowledge.

9. Sect. COMBRETASTRUM Eichl.

Key to the species

- Style exserted.
  - Fruits not more than 3·5 cm. long.
    - Leaves rounded or very obtuse at the apex (rarely slightly acuminate), lateral nerves and reticulation slightly impressed above and scarcely visible beneath; fruit ovoid, 4-ridged. 22. *pyramidatum.*
    - Leaves usually not rounded at the apex (only rounded when abnormal or damaged).
      - Leaves coriaceous, lateral veins and reticulation slightly impressed above and inconspicuous beneath.
        - Leaves rarely exceeding 10 cm. in length, obtuse at the apex; fruit tomentose. 23. *phaeocarpum.*
        - Leaves usually exceeding 12 cm. in length, acute at the apex; fruit lepidote but otherwise glabrous. 24. *laurifolium.*
      - Leaves papyraceous or chartaceous, rarely subcoriaceous, lateral veins usually prominent above and reticulation fairly conspicuous beneath. 25. *laxum.*
  - Fruits 4–5 cm. long.
    - Fruits narrowly winged, 5 cm. long; leaves coriaceous, with a short rounded acumen at the apex and acuminate at the base. 26. *sprucei.*
    - Fruits angled, not winged; leaves papyraceous, acumen usually acute; flowers glabrous. 27. *glabrum.*

Style not exserted (very short); disk minute.
  Leaves ferruginous-pubescent on the nerves beneath. **30**. *brevistylum.*
  Leaves almost glabrous beneath or finely velutinous. **31**. *ulei.*
Species insufficiently known.
  (Jamaica.) **28**. *robinsonii.*
  (British Guiana.) **29**. *fulgens.*

22. Combretum pyramidatum Desv. in Hamilt., *Prodr. Fl. Ind. Occ.*: 35 (1825). Based on a specimen from 'Guiana' in Herb. Desvaux (now in the Paris Herbarium).

Combretum obtusifolium sensu Eichl. in Mart., *Fl. Bras.* xiv, 2: 117 (1867).

Distribution. From Venezuela to Cayenne.

Specimens:

VENEZUELA. Amazonas: near S. Carlos, R. Negro, *Spruce 3691* (BM; K; P; PHD; VH), s.n. (K).

BRITISH GUIANA. R. Rupununi, *Jenman 6792* (K); R. Essequibo, *Schomburgk 55* (BM; Ley; K); R. Essequibo, *A. C. Smith 2689* (K).

SURINAM. Upper R. Coppename, *Boon 1038* (Ut); Upper R. Marowyne, *Kappler 1828* (Ley; P; PHD; Ut; VH); R. Gouini, *Versteeg 56* (Ut).

CAYENNE. Mana, *Mélinon 47* (P); Maroni, *Mélinon 112* (P), *251* (P), s.n. (P); Maroni, *Rech 76* (P); Acarouany, *Sagot 944* (PHD), *944* pro parte (BM; K; P); Ile Portal Bar, *Sagot* s.n. (P); Godebert, *Wachenheim 400* (P). Without precise locality: *Desvaux* s.n. (P, type); *Mélinon* s.n. (P).

This species has commonly been misidentified as *C. obtusifolium* Rich.

23. Combretum phaeocarpum Mart. in *Flora*, xxiv, Beibl. 2: 1 (1841). Based on a plant growing 'in sylvis Prov. Rio Negro', Brazil.

Distribution. Brazil.

Specimens:

BRAZIL. Amazonas: mouth of R. Negro, *Spruce 1759* (BM; P; VH).

I have not seen an authentic specimen of this species but *Spruce 1759* was identified by Eichler as *C. phaeocarpum*. I have not seen enough material to decide whether this is distinct from *C. pyramidatum* to which it is certainly very close.

24. Combretum laurifolium Mart. in *Flora*, xxii, Beibl. 1: 64 (1839). Based on a plant growing by R. Solimões and R. Japura, near Coari and Maribi, Brazil.

Combretum nitidum Spruce ex Eichl. in Mart., *Fl. Bras.* xiv, 2: 118 (1867). Based on *Spruce 1482* and *1846* from near Manáos, Brazil.

Distribution. British Guiana and Brazil.

Specimens:

BRITISH GUIANA. R. Waini, Baramanni Creek, *Forestry Dep. 5056* (K).

BRAZIL. Amazonas: Ega, *Poeppig 2493* (P), s.n. (BM); near Barra, R. Negro, *Spruce 1327* (K; PHD); *1482* (BM; P; PHD; VH); *1846* (BM; PHD), s.n. (BM; VH); R. Negro, *Spruce 1575* (BM; K; P; PHD), *1740* (BM; K; PHD). Pará: near Pará, *Burchell 9571* (K; P). Rio de Janeiro: Quinta de S. Christovão (cultivated), *Glaziou 13802* (P).

This species has coriaceous, oblong-lanceolate leaves up to 20 cm. long and ellipsoid, rather narrowly winged fruits up to 3 cm. long. *Spruce 1482* has very small fruits, about 7 mm. long. These are probably galled.

25. Combretum laxum Jacq., *Enum. Pl. Carib.*: 19 (1760). Based on a plant from S. Domingo. A fragmentary specimen in the British Museum Herbarium may be either the type or part of the type-collection. [Fig. 4*c–e*.]

Combretum puberum Rich. in *Act. Soc. Hist. Nat. Par.* i: 108 (1792). Based on a specimen collected by Le Blond in Cayenne.

Combretum obtusifolium Rich., loc. cit. No type is cited but an unnumbered specimen from Cayenne collected by Richard is probably the type.

Combretum mexicanum Bonpl., *Pl. Aequinox.* ii: 159, t. 132 (1809). Based on a plant collected by Humboldt and Bonpland near Acapulco in Mexico.

Forsgardia laevis Vell., *Fl. Flum.*: 152 (1825), op. cit. iv: t. 13 (1827). Based on a plant collected 'in sylvis maritimis Regii Praedii S. Crucis', near Rio de Janeiro, Brazil.

Combretum odoratum Pav. ex Don in *Trans. Linn. Soc. Lond.* xv: 430 (1827). Based on a specimen collected by Pavon in Ecuador.

Combretum cordatum Don, tom. cit.: 440 (1827). Based on a specimen collected by Swartz in Hispaniola.

Combretum ferrugineum Don, loc. cit. Based on a specimen from S. America in Herb. Banks (not seen).

Combretum bugi Cambess. in St-Hil., Juss. & Cambess., *Fl. Bras. Merid.* ii: 247, t. 130 (1829). Based on a plant collected near Rio de S. Francisco, Minas Geraes, Brazil.

Chrysostachys ovatifolia Pohl, *Pl. Bras.* ii: 66, t. 143 (1831). Based on a plant from R. Reazão, Brazil.

Combretum variabile Mart. in *Flora*, xxii, Beibl. 1: 62 (1839). Based on Brazilian specimens (and possibly one from Cayenne) collected by Martius and included under the three varietal epithets *angustifolium*, *oblongifolium* and *detersum*.

Combretum variabile var. *angustifolium* Mart., loc. cit. Based on a plant growing near Tijuca, near Sebastianopolis, Brazil.

Combretum variabile var. *oblongifolium* Mart., tom. cit.: 63 (1839). Based on a plant growing near Ilheos, Brazil.

Combretum variabile var. *detersum* Mart., loc. cit. Based on a plant growing near R. Japura and R. Negro in Brazil, and in Cayenne.

Combretum pulchellum Mart., tom. cit.: 64 (1839). Based on specimens from near Pará, Brazil.

Combretum ferrugineum Hoffmansegg ex Mart., loc. cit. nom. nud. Based on *Martius 578*.

Combretum adenophyllum Mart. in *Flora*, xxiv, Beibl. 2: 1 (1841). Based on specimens collected by Martius near Cuyabá, Brazil.

Combretum terminalioides Steud. in *Flora*, xxvi, 2: 762 (1843). Based on *Hostmann & Kappler 1153* from Surinam.

Combretum jacquinii Griseb., *Fl. Brit. W. Ind.*: 275 (1860) nom. illegit. Based on *C. laxum* Jacq.

Combretum viscidum Wright ex Griseb., *Cat. Pl. Cub.*: 109 (1866). Based on *C. Wright 2574* from Cuba.

Combretum jacquinii f. *laxum* (Jacq.) Eichl. in Mart., *Fl. Bras.* xiv, 2: 115 (1867). Based on *C. laxum* Jacq.

Combretum jacquinii f. *brasiliense* Eichl. in Mart., tom. cit.: 116 (1867). Based on *C. variabile* Mart., *Herb. Fl. Bras. 511* (*1*) in part.

Combretum jacquinii f. *bugi* (Cambess.) Eichl. in Mart., loc. cit. Based on *C. bugi* Cambess.

Combretum jacquinii f. *ovatifolium* (Pohl) Eichl. in Mart., loc. cit. Based on *Chrysostachys ovatifolia* Pohl.

Combretum jacquinii f. *pulchellum* (Mart.) Eichl. in Mart., loc. cit. Based on *C. pulchellum* Mart.

Combretum accedens Heurck & Muell. Arg. in Heurck, *Obs. Bot.*: 234 (1870). Based on a plant from 'Guiana', collector unspecified.

Combretum odoratissimum Sesse & Moc., *Fl. Mex.* ed. 2: 90 (1894). Based on a plant growing in the mountains of Tepalcatepeque and Coahuayana, Mexico.

Combretum jacquinii var. *laxum* (Jacq.) Pulle, *Enum. Pl. Surin.*: 342 (1906) nom. illegit. Based on *C. laxum* Jacq.

Combretum jacquinii var. *pulchellum* (Mart.) Pulle, loc. cit. Based on *C. pulchellum* Mart.

Combretum epiphyticum Pittier in *Contrib. U.S. Nat. Herb.* xviii: 247 (1917). Based on *Pittier 6819* from the Canal Zone, Panama.

Combretum oblongifolium Rusby, *Descr. New Sp. S. Amer. Pl.*: 70 (1920). Based on *H. H. Smith 1947* from Colombia.

Combretum marchii Fawc. & Rendle in *J. of Bot.* lxiii: 115 (1925). Based on a specimen collected by March in Jamaica.

Combretum brunnescens Gleason in *Bull. Torrey Bot. Cl.* liii: 291 (1926). Based on *De La Cruz 3566* from R. Amakura, British Guiana.

DISTRIBUTION. Widespread from Mexico to northern Argentina.

SPECIMENS:

MEXICO. NAYARIT: Laguna del Mamey, *Ortega 105* (US). VERA CRUZ: Fortuno, *Williams 8987* (K). COLIMA: Manzanillo Bay, *Hinds* s.n. (K); Manzanillo, *Jones 438* (US); Manzanillo, *Palmer 1374* (BM; K; US). MICHOACAN or GUERRERO: La Baranca, *Langlassé 129* (K; US), *130* (K; US); R. Coyaquella, *Langlassé 833 bis* (K). GUERRERO Acapulco, *Beechey* s.n. (K); near Acapulco, *Bonpland 3866* (P, probably type of *C. mexicanum*), s.n. (P); Acapulco, *Palmer 377* (BM; K; P; US). OAXACA: between Calotepec and Cazautepec, *Nelson 2455* (US); Cafetal Concordia, 650 m. alt., *Akrinius*? *648* (US). TABASCO: Tenosique, Boca Cerro, *Matuda 3537* (K).

BRITISH HONDURAS. R. Northern, Yucatan, *Gentle 1285* (K); El Cayo District, Vaca, *Gentle 2600* (K); Stann Creek, *Robertson 288* (BM); Middlesex, 65 m. alt., *Schipp 356* (BM; K). Without precise locality: *Peck 744* (K), *880* (K); *Schipp 768* (K).

GUATEMALA. ALTA VERA PAZ: near Finca Sepacuite, *Cook & Griggs 648* (US); EL PETEN: S. Teresa, R. Subin, *Lundell 2675* (BM). IZABAL: Izabal, *Blake 7847* (US); Boca del Polochic, *D. Smith 1707* (K; US).

HONDURAS. S. Barbara: S. Pedro Sula, alt. 200 m., *Thieme 5619* (K; US). ATLANTIDA: La Ceiba, *Yete 8254* (K); Coyoles, Yoro, *Yuncker, Koepper & Wagner 8059* (K).

NICARAGUA. R. Jesus, *Brenes 14529* (US).[1] Without precise locality. *C. Wright* s.n. (US).

PANAMA. CANAL ZONE: Quebrada Tranquilla, alt. 70–80 m., *Dodge & Allen 17501* (BM; K); near Gatun, *Hayes 7* (US); Frijoles, *Hayes 54* (BM), s.n. (K); Caño Quebrado, *Pittier 6668* (US), *6810* (US, type of *C. epiphyticum*). Without precise locality, *Hayes 771* (NY); *Seemann 1658* (BM).

WEST INDIES. CUBA: Mata, *C. Wright 2574* (BM, type of *C. viscidum*; K; P). S. DOMINGO: *Beauvois* s.n. (P); *Herb. Desétang 48* (PHJ); *Delport* s.n. (PHJ); *Eggers 1525* (BM; K; P), *2431* (BM; K); *Jacquin* s.n. (BM, type of *C. laxum* ?); *Poiteau 641* (BM), s.n. (P; PHC; PHJ); *Richard* s.n. (P); R. Macoris, *Taylor 255* (BM). Hispaniola without precise locality: *Schomburgk 106* (K); *Swartz* s.n. (BM, two specimens, the one with larger leaves being the type of *C. cordatum*). JAMAICA: *March* s.n. (K, type of *C. marchii*). TRINIDAD: *Lockhart* s.n. (K).

COLOMBIA. Near Lake Sapatoza, Magdalena Valley, *Allen 352* (K); New Grenada, S. Blas, *Barclay 9* (VH); Goajira, *Dawe 535* (K); Megua, near Barranquilla, *Elias 1073* (BM); Utiacuri, near Barranquilla, *Elias 1328* (BM); El Magdalena, about 25 km. N.E. of Chiriguana, *Haught 2250* (BM); Torrecilla, near Turbaco, Bolivar, *Killip & Smith 14680* (BM); Sierra del Macarena, R. Guapaya, *Philipson, Idrobo & Fernandez 1630* (BM); S. Marta, *H. H. Smith 883* (K; US), *885* (BM; K; Mu; P; PHD; US), *1947* (Ley; K; St; US), *1948* (BM; Ley; K; PHD; US). Without precise locality: *Triana* s.n. (P).

VENEZUELA. Temblador, Medio Caura, alt. 100 m., *Williams 11558* (BM).

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[1] A doubtful specimen. The fruits are probably galled.

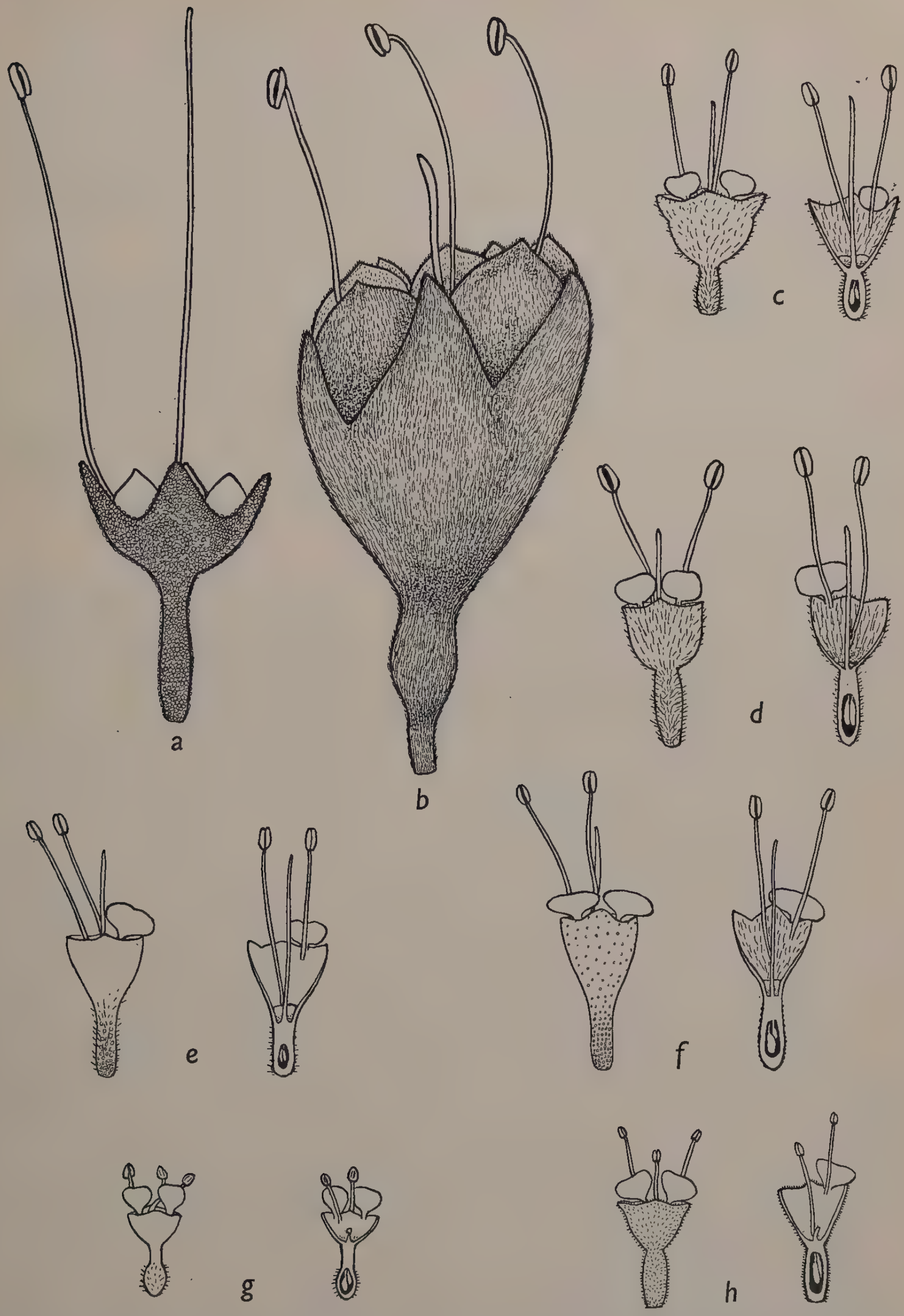

Fig. 4. Diagrams of flower structure. (*a–b*, × 2½; *c–h*, × 5.) (*a*) *Combretum lanceolatum* Pohl (*Chase 2807*); (*b*) *C. cacoucia* Exell (*Schomburgk 272*); (*c*) *C. laxum* Jacq. (*Pittier 6819*); (*d*) *C. laxum* Jacq. (type of *C. accedens*); (*e*) *C. laxum* Jacq. (*H. H. Smith 1947*, type of *C. oblongifolium* Rusby); (*f*) *C. glabrum* DC. (*Gleason 338*, type of *C. fusiforme* Gleason); (*g*) *C. brevistylum* Eichl. (*Poeppig* s.n.); (*h*) *C. ulei* Exell (*Ule 5075*).

BRITISH GUIANA. R. Barima, *De la Cruz 3425* (K); R. Waina, *De la Cruz 3585* (K; US); Kamakusa, Upper R. Mazaruni, *De la Cruz 4528* (US); Kaieteur Falls, R. Potaro, *De la Cruz 4460* (US); Mazaruni Station, *Forest Dep. 4138* (K); R. Essequibo, *Forest Dep. 6162* (K); R. Corentyne, *Jenman 99* (P); Upper R. Demerara, *Jenman 4023* (US); R. Mazaruni, *Jenman 5332* (BM); R. Demerara, *Jenman 5334* (BM); Upper R. Mazaruni, *Leng 124* (NY), s.n. (NY); Kaieteur Plateau, *Maguire & Fanshawe 23355* (K); Demerara, *Parker* s.n. (K); Mazaruni Station, *Sandwith 1551* (BM; K); Roraima, *Schomburgk 509* (BM; K; P); R. Pomeroon, *Schomburgk 1480* (P); R. Kuyuwini, *A. C. Smith 2566* (K), *2595* (K); Shodikar Creek, *A. C. Smith 3019* (K); R. Corentyne, *im Thurn* s.n. (K; P). Without precise locality: *Appun 862* (K), *1722* (K); *Jenman 2237* (K), *3783* (K), *4648* (K), *4906* (K), *7339* (K); *Schomburgk 872* (BM; K; P).

SURINAM. Upper R. Nickerie, *Boschwezen 1033* (Ut); Kaboerie Forest Reserve, *Boschwezen 2976* (Ut); R. Maratacca, *Boschwezen 3481* (Ut); Upper R. Saramacca, Toekoemoetoe Creek, *Boschwezen 5707* (BM; Ut); Bergendaal, *Focke 355* (Ley); near Paramaribo, *Focke 832* (Ley); Pauluskreek, *Focke 1416* (Ley); Suriname, *Hostmann 138* (BM; K; P; Ut), *1153* (K), s.n. (P; US; Ut); R. Marowyne, near Arminafalls, *Lanjouw 522* (Ut); R. Suriname, near Goddo, *Stahel 155* (BM); R. Corentyne, *Stahel & Gonggryp 219* (K); Upper R. Suriname, *Tresling 3* (Ut); R. Tapanahoni, *Versteeg 612* (Ut), *746* (Ut); Upper R. Suriname, *Wullschlaegel 1324* (Br; Go). Without precise locality: *Focke* s.n. (P); *Hostmann & Kappler 1153* (Caen); *Kegel 259* (Go; Ut); *Kickx* s.n. (Caen; P); *Menge* s.n. (Br); *Voltsz* s.n. (Br).

CAYENNE. Gourdonville, *Benoist 1511* (P); La Mana, *Mélinon 2* (P), *770* (P); R. Maroni, *Mélinon 291* (P); Karouany, *Sagot 1* (P), *241* (BM; Caen; K; P), *255* (Caen). Without precise locality: *Le Blond* s.n. (PHL, two specimens of which one is the type of *C. puberum*); *Leprieur* s.n. (P); *Martin 59* (BM), *69* (BM), s.n. (BM); *Richard* s.n. (P, two specimens one of which is the type of *C. obtusifolium*).

BRAZIL. Rio Branco: Surumu, Serra do Mel, *Ule 8329* (Ley; K). Amazonas: R. Maturaca, below Salta de Hua, *Holt & Blake 523* (US); near Barra, R. Negro, *Spruce 1966* (K), s.n. (P); mouth of R. Solimões, *Spruce 1646* pro parte (K). Acre Territory: mouth of R. Tarauaca, *Krukoff 4607* (K); R. Macauhau, *Krukoff 5460* (K), *5727* (K); R. Solimões, *Krukoff 8247* (K), *8404* (K); S. Paulo de Olivença, *Krukoff 8718* (BM; K); R. Acre, *Ule 9665* (Ley). Pará: Pará, *Burchell 9967* (K; P); R. Embira, *Krukoff 4790* (K), *4964* (BM); Humayta, *Krukoff 6267* (K), *6610* (K); near Ilheos, *Martius 410* (Type of *C. variabile* var. *oblongifolium*; BM; Ley; K; P; VH); R. Acara, *Mexia 5979* (BM); Ilheos, *Moricand* s.n. (K); Pará, *Spruce 217* (PHD); opposite Ilha de Marunarituba, *Spruce 409* (K; PHD); between Santarem and Obidos, *Spruce 419* (K; PHD), s.n. (BM; K); Santarem, *Spruce 1079* (K); near Santarem, *Spruce* s.n. (BM; K; VH); near Pará, *Spruce* s.n. (BM; VH); Prainha, *Traill 218* (K). Piauhy: R. Gurgea, *Gardner 2568* (BM; Caen; K; P; PHD; US). Pernambuco: Pernambuco, *Forisell 169* (St); R. Capibariba, *Gardner 994* (BM; Caen; K; P; PHD); Tapera, *Pickel 137* (BM). Ceará: R. Maranguapinha, *Drouet 2343* (K). Matto Grosso: near Cuyabá, *Martius 578* (Type of *C. adenophyllum*; BM; Ley; P); *Weddell 3429* (P). Goyaz: near Goyaz, *Burchell 6361* (K), *7294* (K; NY; P; US). Bahia: Bahia, *Blanchet 9* (P), *726* (BM), *1558* (BM; PHD), *2720* (PHD), s.n. (PHD); Utinga, *Blanchet 1759* (BM; K; P); Serra Jacobina, *Blanchet 3234* (BM; PHD); *Blanchet 1517* (BM), *1717* (BM), *2115* (BM), *2172* (BM), *3261* (PHD); *Moricand* s.n. (PHD). Minas Geraes: Lagoa Santa, *Claussen 106* (K); *Claussen 75* (NY; P), *104* (P), s.n. (K); Natividade, *Gardner 3140* (K); S. Terezinha, *Macedo 1915* (BM), *2489* (BM); *St-Hilaire 1844* (P); Lagoa Santa, *Warming* s.n. (P). Rio de Janeiro: near Rio de Janeiro, *Burchell 2616* (K), *2734* (K; P); Corcovado, *Glaziou 3948* (K; P); Larangeiras, *Glaziou 7607* (K; P); Mana, *Glaziou 8338* (K; P), *8339* (K; P); *Glaziou 8669* (K; P); *Glaziou 10717* (K; P); Orga Mts., *Jellicoe 4096* (K); *Riedel* s.n. (Caen). Without precise locality: *Glaziou 589* (P); *Gomez* s.n. (K); *Martius 119* (Ley); *Pohl 1484* (K); *Riedel 24* (P); *Riedel 406* (K), in *Herb. Hance 5748* (BM; PHC), s.n. (US); *Sello 443* (P).

ECUADOR. Guayas: Guayaquil, *Pavon* s.n. (BM, type of *C. odoratum*; P).

PERU. Loreto: Quitos, *Killip & Smith 27125* (BM); Florida, alt. 180 m., *Klug 2237* (BM; K); Fortaleza, near Yurimaguas, *Klug 2780* (BM; K); Maquisapa, Upper R. Nanay, *Williams 1195* (US).

BOLIVIA. Junction of R. Beni and R. Madre de Dios, *Rusby 721* (BM; K; PHC; US).

PARAGUAY. R. Paraguay, *Balansa 2337* (BM; K); near Concepción, *Hassler 7304* (BM; K; P); Central Paraguay, *Morong 822* (BM; K; US).

ARGENTINA. Misiones: R. Paraná, *Ekman 1726* (St). Formosa: *Jorgensen 2062* (US).

Without locality or collector (VH, type of *C. accedens*).

As here delimited this species is extremely polymorphic, and it may be possible eventually to treat it in a more satisfactory manner. It can be divided into about fourteen 'varieties' but many of the characters depend on the fruit and, unfortunately, but few fruiting specimens are available and but little information in the way of field-notes.

The type of *C. laxum* came from S. Domingo and all that I have seen of it is a tiny fragment of an inflorescence in the British Museum Herbarium. *Eggers 1525* (BM) and *2431* (BM) from S. Domingo are probably identical.

The rest of the West Indian material is fairly homogeneous except for *Swartz* s.n. from 'Hispaniola', the type of *C. cordatum*, which has much broader leaves and a tomentose rhachis (lepidote but otherwise almost glabrous in Jacquin's specimen), and *March* s.n. from Jamaica, the type of *C. marchii*, with much narrower leaves. Specimens very similar to this latter have also been collected in Brazil.

In Brazil the species reaches its maximum variability and is referred to by Eichler as 'Stirps maximopere variabilis'. *Chrysostachys ovatifolia* Pohl, with suborbicular, rather coriaceous leaves, is the most distinct form and might be separated specifically were it not for some transitional forms difficult to classify.

An eventual understanding of this 'species' and its possible division or subdivision will probably depend on the collection of far more fruiting material, for the comparatively few fruits which we have differ from each other considerably in size and shape and especially in the width of the wings. The presumably typical S. Domingo material has fairly broad-winged fruits, with wings about 5 mm. broad, but some fruits are known with quite narrow, rigid wings. Such a small percentage of the specimens is in fruit that to base a classification on the fruit would, at present, have no practical advantage. It is essential to correlate differences in the fruit with differences in the flower and indumentum (if any such correlation exist) before progress can be made. Meanwhile, there is little advantage in making new names for specimens which come within this 'complex'; for a glance at the long synonymy will show that in all probability valid names are already in existence for any taxa which may eventually be separated, if the problem is ever elucidated.

26. **Combretum sprucei** Eichl., in Mart., *Fl. Bras.* xiv, 2: 115 (1867). Based on *Spruce 3483* from S. Carlos, Venezuela.

Distribution. Venezuela.

Specimens:

VENEZUELA. Amazonas: S. Carlos, *Spruce 3483* (Type; BM; K; P; PHD).

27. **Combretum glabrum** DC., *Prodr.* iii: 19 (1828). Based on a specimen from Cayenne preserved in De Candolle's herbarium in Geneva. [Fig. 4*f*.]

Combretum fusiforme Gleason in *Bull. Torrey Bot. Cl.* liii: 292 (1926). Based on *De la Cruz 4104* from the Upper R. Mazaruni, British Guiana.

Distribution. British Guiana and Cayenne.

SPECIMENS:

BRITISH GUIANA. Upper R. Mazaruni, *De la Cruz 4104* (US, type of *C. fusiforme*); Hacket Creek, *Forestry Dep. 5058* (K); R. Potaro, Lower R. Waini, Tumatumari, *Gleason 338* (K; NY; US), *397* (NY; US); Roraima, *Schomburgk 871* (BM; K; P); R. Pomeroon, without collector (US).

CAYENNE. *Richard* s.n. (P); *von Rohr 435* (BM); without collector or number (DC, type of *C. glabrum*).

This species is distinguished by the long, narrow, angled fruit, but in flower it is not easy to separate from some of the forms of *C. laxum*. The inflorescences are, however, usually more lax and less hairy than in most of the specimens referred to *C. laxum*; but, as regards the latter character, there is no certain means of separation, for the fragment of the type of *C. laxum* has very sparse pubescence. The type in the De Candolle Herbarium may be the same gathering as *Richard* s.n. (P).

28. **Combretum robinsonii** Fawc. & Rendle in *J. of Bot.* lxiii, 115 (1925); *Fl. Jam.* v: 312, fig. 123, D (1926). Based on drawings by Robinson, a description by Macfadyen and a specimen collected by Harris in Jamaica.

DISTRIBUTION. Jamaica.

SPECIMENS:

None seen.

This species is insufficiently known but it may prove to be *C. laxum* Jacq. There is a photograph in the British Museum Herbarium of a specimen collected by W. Harris on the bank of the R. Black, between Lacovia and Elam Wharf, Jamaica.

29. **Combretum fulgens** Gleason in *Bull. Torrey Bot. Cl.* liii: 292 (1926). Based on *De la Cruz 4129* from the Upper R. Mazaruni, British Guiana.

DISTRIBUTION. British Guiana.

SPECIMENS:

BRITISH GUIANA. Upper R. Mazaruni, Kamakusa, *De la Cruz 4129* (US, type).

All the fruits on the specimen are galled. In the absence of flowers the species is difficult to place but it appears to be allied to, or perhaps identical with, *C. laxum*.

30. **Combretum brevistylum** Eichl. in Mart., *Fl. Bras.* xiv, 2: 118, t. 34, fig. 14 (1867). Based on *Poeppig 2494* from Amazonas, Brazil. [Fig. 4*g*.]

DISTRIBUTION. Northern Brazil.

SPECIMENS:

BRAZIL. AMAZONAS: *Poeppig 2494* (Type; VH); *Poeppig* s.n. (BM).

31. **Combretum ulei** Exell, sp.nov. [Fig. 4*h*.] *Frutex* scandens, ramulis primo velutinis demum fere glabris. *Folia* opposita petiolata, petiolo ad 6–8 mm. longo velutino, lamina coriacea vel subcoriacea ovato-elliptica, ad 16 × 8 cm., supra fere glabra subtus punctulata fere glabra sinu parvo deltoideo instructa, costa media minutissime velutina excepta, apice abrupte longe acuteque acuminata, basi rotundata, costa media supra impressa subtus prominente, costis lateralibus utrinsecus 6–8 supra impressis subtus prominentibus. *Flores* tetrameri sessiles parvi, in paniculas valde ramosas terminales et axillares dispositi, rhachide fulvo-velutina. *Receptaculum* superius cupuliforme, 1·2 × 2 mm., extra fulvo-velutinum, inferius 1–1·5 mm. longum fulvo-velutinum. *Calycis lobi* minuti vel 0. *Discus* 0. *Stamina* 8, biserialia, 4 petalis opposita, 2 mm. longa, 4 basin receptaculi versus inserta, 2·2 mm. longa. *Stylus* 0·2–0·3 mm. longus. *Ovula* 2. *Fructus* ignotus.

DISTRIBUTION. Northern Brazil.

SPECIMENS:

BRAZIL. AMAZONAS: Marary, R. Jurua, *Ule 5075* (Ley; K, type).

In general appearance this species resembles *C. laxum*, though the flowers are somewhat smaller and the indumentum is different, the branchlets, midribs and rhachides being very finely velutinous. The flowers, however, closely resemble those of *C. brevistylum* in structure but the style is even shorter. As in *C. brevistylum*, the disk is absent. *C. brevistylum* also differs in having a rather coarsely pubescent, almost pilose indumentum.

10. Sect. Terminaliopsis Ridl.

32. **Combretum rupicola** Ridl., in *J. Linn. Soc. Bot.* xxvii: 28 (1890). Based on *Ridley, Lea & Ramage 59* from Fernando Noronha.

Distribution. Fernando Noronha.

FERNANDO NORONHA. *Ridley, Lea & Ramage 59* (BM, type; K).

This interesting plant is a very aberrant species differing from a typical *Combretum* in being dioecious and in having no petals (at least as far as the female flowers are concerned). Ridley (loc. cit.) describes the ovary as having a single, erect ovule, but this is an error for there are two pendulous ovules, the typical arrangement in the genus. The affinity of the species seems to be with Sect. *Combretastrum* to the species of which it has a close resemblance in general appearance.

11. Sect. Spinosae Exell

Key to the species

Leaves pubescent or glabrous beneath.
  Upper receptacle glabrous or nearly so; lower receptacle glabrous or patent-pubescent.
    Lower receptacle glabrous or loosely patent-pubescent. **33.** *decandrum.*
    Lower receptacle appressed-pubescent. **34.** *spinosum.*
  Upper receptacle densely appressed-pubescent; lower receptacle densely sericeous. **35.** *rovirosae.*
Leaves ferruginous-tomentose beneath. **36.** *pavonii.*

33. **Combretum decandrum** Jacq., *Enum. Pl. Carib.*: 19 (1760); *Select. Stirp. Amer. Hist.* 104 (1763); op. cit. ed. fol. imp.: 52, t. 260, fig. 27 (*c.* 1780). Based on a plant growing at Cartagena, Colombia. [Fig. 5*a–c*.]

Combretum alternifolium Pers., *Syn.* i: 412 (1805) nom. illegit. Based on *Combretum decandrum* Jacq.

Gonocarpus jacquinii Hamilt., *Prodr. Fl. Ind. Occ.*: 39 (1825) nom. illegit. Based on *Combretum decandrum* Jacq.

Poivrea alternifolia (Pers.) DC., *Prodr.* iii: 17 (1828) nom. illegit. Based on *Combretum alternifolium* Pers.

Combretum palmeri Rose in *Contrib. U.S. Nat. Herb.* v: 136 (1897). Based on *Palmer 396* from Guerrero, Mexico.

Combretum nicoyanum Pittier in *Contrib. U.S. Nat. Herb.* xviii: 247 (1917). Based on *Tonduz 13503* from Nicoya, Mexico.

Combretum latipaniculatum Rusby, *Descr. New Sp. S. Amer. Pl.*: 69 (1920). Based on *H. H. Smith 2101* from S. Marta, Colombia.

Distribution. From Mexico to Colombia.

Specimens:

MEXICO. Mexico: Temascaltepec, Ixtapan, *Hinton 3018* (K); Temascaltepec, Acatitlan, *Hinton 3172* (BM; K); Temascaltepec, Bejucos, *Hinton 3390* (BM; K). Guerrero: Coyuca, Pungarabato, *Hinton 5475* (BM; K); Acapulco, *Palmer 396* (BM; K; P; US, type of *C. palmeri*); Achotla, *Reko 4916, 5106* (US).

GUATEMALA. Retalhulei: *Bernoulli & Cario 2982* (K; St). Chiquimula: between Chiquimula and Jocatan, *Seler 3311* (K; US).

COSTA RICA. Guanacaste: Nicoya, *Tonduz 13503* (BM; K; US, type of *C. nicoyanum*).

PANAMA. Canal Zone: Empire Station, *Hayes 31* (BM; K; P). Darien: Patino, *Pittier 6607* (US). Without precise locality: *Seemann 614* (BM).

COLOMBIA. S. Marta: *H. H. Smith 2101* (Ley; K; US, type of *C. latipaniculatum*) Colombia? 'Isla de Aquiana, New Grenada', *Seemann 6141* (K).

Vernacular name. Mostrinco (Costa Rica).

34. **Combretum spinosum** Bonpl., *Pl. Aequinox.* ii: 161 (1809). Based on a plant growing on the banks of the R. Orinoco, probably represented by *Bonpland 1118* in Bonpland's herbarium, Paris. [Fig. 5*d*.]

Combretum guayca Humb., *Rel. Hist.* iii: 3 (1825) nom. nud. Based on the same type as *C. spinosum.*

Poivrea eriopetala DC., *Prodr.* iii: 18 (1828). Based on specimens collected in S. Domingo and Cuba preserved in De Candolle's herbarium.

Combretum eriopetalum (DC) Don, *Gen. Syst.* ii: 665 (1832). Based on *Poivrea eriopetala* DC.

Combretum punctulatum Pittier in *Contrib. U.S. Nat. Herb.* xviii: 248 (1917). Based on *Pittier 4002* from R. Trinidad, Panama.

Combretum jacquinii sensu Williams in *Tropical Woods*, 68: 37 (1941).

Distribution. Panama, Venezuela and in the West Indies from Cuba to Trinidad.

Specimens:

PANAMA. Canal Zone: R. Trinidad, *Pittier 4002* (US, type of *C. punctulatum*).

WEST INDIES. Cuba: fide De Candolle (no specimen seen). S. Domingo: fide De Candolle (no specimen seen). St Vincent: *Guilding* s.n. (K). Trinidad: *Lockhart* s.n. (K); *Purdie* s.n. (K); *Riedlé* s.n. (PHJ); *Herb. Richard* s.n. (PHD). West Indies without precise locality, *von Rohr* s.n. (BM).

VENEZUELA. Bolivar: Angostura (Ciudad Bolivar), *Bonpland 1118* (PHB, type). Caicara, *Williams 13271* (K). Caracas: La Guaira, *Moritz 1689* (BM; Cop). Cojedes: between El Tinaco and S. Carlos, *Pittier 11691* (US). Merida: *Fendler 2315* (K). Zulia: Maracaibo, *Plée* s.n. (P). Without precise locality: *de Grosourdy* s.n. (P).

Vernacular name. Guaica, Guayca or Bejuco Guaica (Venezuela).

According to Williams (loc. cit.) this species is a woody vine with spines up to 2–5 cm. long.

Moritz 1689 is tetramerous but does not seem to differ in any other way. Tetramerous flowers are not uncommonly found in several normally pentamerous species of *Combretum.*

35. **Combretum rovirosae** Exell, sp.nov. [Fig. 5*e*.] *Frutex* scandens? ramulis breviter appresse pubescentibus. *Folia* alternata vel subopposita petiolata, petiolo 1 cm. longo appresse pubescente demum basi spinam formante, lamina elliptica apice basique acuta, ad 7 × 3·5 cm., supra minute verruculosa fere glabra subtus minutissime lepidota et ad nervos sparse puberula ceteroqui glabra, costis lateralibus utrinsecus 6–8. *Flores* parvi tetrameri sessiles in spicas elongatas paniculatas dispositi. *Receptaculum* superius cupuliforme dense appresse pubescens, 1·5 × 2·2 mm., inferius (calycis lobis inclusis) 1·5 mm. longum, dense sericeum. *Calycis lobi* deltoidei, 0·8 × 0·9 mm. *Discus* parvus margine pilosus. *Petala* obovate-spathulata, 1·8 × 1·2 mm., sericeo-tomentosa. *Stamina* exserta, filamentis 2·3 mm. longis. *Stylus* exsertus, 3 mm. longus, glaber. *Fructus* ignotus.

Distribution. Mexico and Honduras.

Specimens:

MEXICO. Tabasco: Boca Cerro, Tenosique, *Matuda 3532* (K); 'En el Macayal', *Rovirosa 206* (K, type; US). Chihuahua: 'Inter amnem fluminis Rio del Carrizal dictum et pagum Alasta', *Rovirosa 612* (K; US).

HONDURAS. Atlantida: Cuba, *Yuncker, Koepper & Wagner 8254* (K); R. Salado, *Yuncker, Koepper & Wagner 8332* (K); Mt. Cangrejal, *Yuncker, Koepper & Wagner 8426* (K).

Vernacular name. Chanaque (Mexico).

This species is distinguished from *C. decandrum* by the densely sericeous receptacle and the distinctly smaller, tetramerous flowers.

36. Combretum pavonii Don in *Trans. Linn. Soc. Lond.* xv: 436 (1827). Based on a specimen collected by Pavon at Guayaquil. [Fig. 5*f*.]

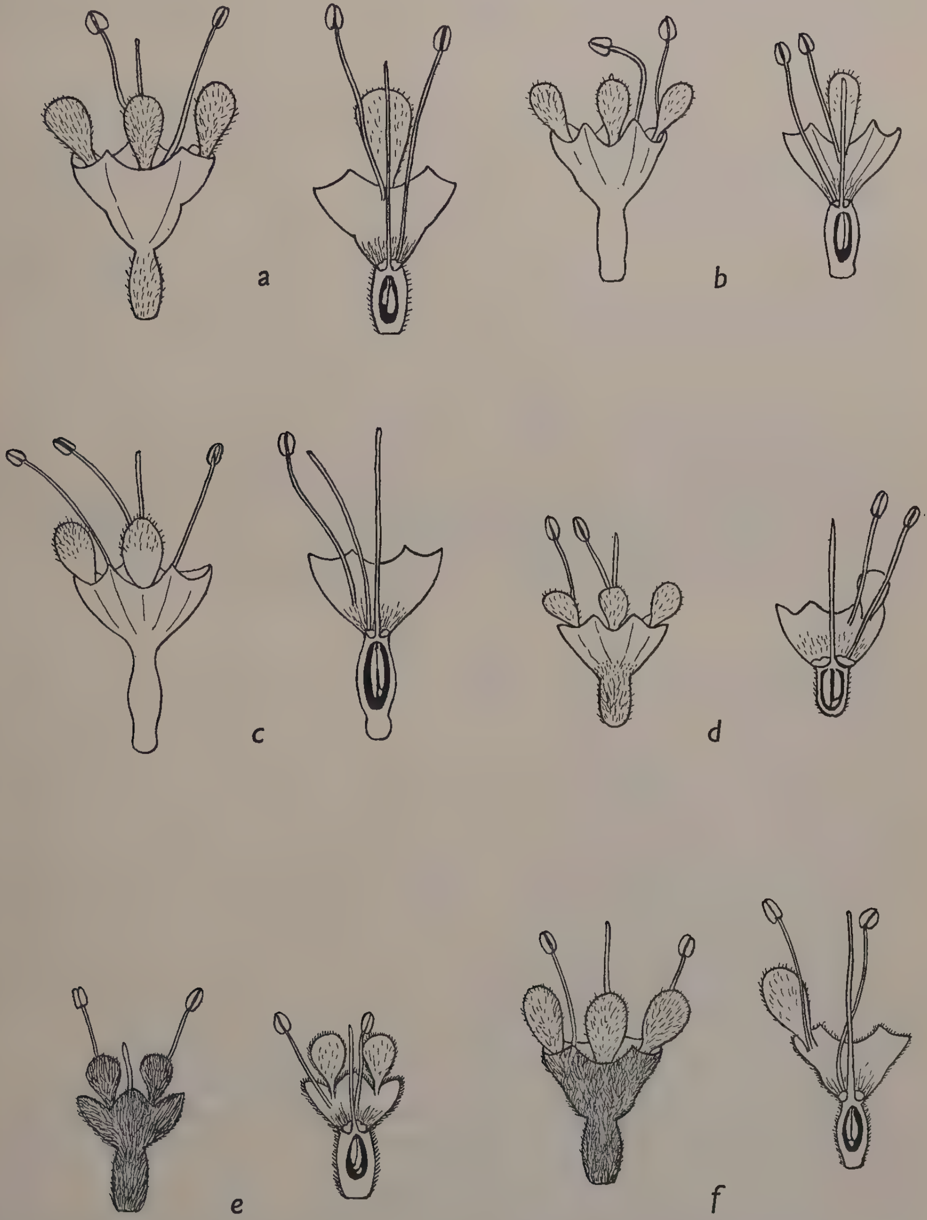

Fig. 5. Diagrams of flower structure. (All × 5.) (*a*) *Combretum decandrum* Jacq. (*H. H. Smith 101*, type of *C. latipaniculatum* Rusby; (*b*) *C. decandrum* Jacq. (*Tonduz 13503*, type of *C. nicoyanum* Pittier); (*c*) *C. decandrum* Jacq. (*Palmer 396*, type of *C. palmeri* Rose); (*d*) *C. spinosum* Bonpl. (*Pittier 11691*); (*e*) *C. rovirosae* Exell (*Rovirosa 206*); (*f*) *C. pavonii* Don (*Pavon* s.n.).

Combretum decandrum Ruiz & Pav. ex Don, loc. cit. nom. synon. The name was probably originally intended merely as an identification of the plant as *C. decandrum* Jacq.

Poivrea pavonii (Don) Walp., *Rep. Bot. Syst.* ii: 64 (1843). Based on *Combretum pavonii* Don.

DISTRIBUTION. Ecuador.

SPECIMENS:

ECUADOR. GUAYAS: Guayaquil, *Pavon* s.n. (BM, type); R. Daule, near Guayaquil, *Spruce 6255* (BM; K; NY; St).

SPECIES INSUFFICIENTLY KNOWN

37. **Combretum barbatum** Don [ex Loud., *Hort. Brit.*: 157 (1830) nom. nud.] *Gen. Syst.* ii, 665 (1832). Based on a plant introduced into England in 1820 and said to be a native of Maranhão, Brazil.

Poivrea barbata (Don) Walp., *Rep. Bot. Syst.* ii: 64 (1843). Based on *Combretum barbatum* Don.

According to the description this is a species with rather large, pentamerous flowers in panicles and white, bearded petals. I cannot identify it with any known Brazilian species of *Combretum*.

OLD WORLD SPECIES CULTIVATED IN THE WESTERN HEMISPHERE

38. **Combretum coccineum** (Sonner.) Lam., *Encyc. Méth.* i: 734 (1785). Based on *Cristaria coccinea* Sonner.

Cristaria coccinea Sonner., *Voy. Ind. Or.* 247: t. 140 (1782). Based on a plant brought from Madagascar and cultivated in Mauritius.

Grislea coccinea (Sonner.) Britton in Britton & Wilson, *Scient. Survey of Porto Rico and Virgin Is.* vi: 25 (1925). Based on *Cristaria coccinea* Sonner.

DISTRIBUTION. Native of Madagascar.

SPECIMENS:

WEST INDIES. VIRGIN IS.: St Thomas, *N. L. Britton, E. G. Britton & Kemp 8* (K). TRINIDAD: fide Williams (Williams & Williams Jr., *Useful & Ornam. Pl. Trin. & Tob.* ed. 3: 110 (1941)).

39. **Combretum ovalifolium** Roxb. [*Hort. Beng.* [28] (1814) nom. nud.] *Fl. Ind.* ii: 226 (1832). Based on a plant from Coromandel, India.

DISTRIBUTION. Native of India.

SPECIMENS:

WEST INDIES. TRINIDAD: Botanic Gardens, *Broadway 7001* (K), *10095* (K); Govt. House grounds, *Hart 7007* (K).

40. **Combretum paniculatum** Vent., *Choix Pl.*: sub t. 58 (1803). Based on a plant collected by Roussillon in Senegal.

DISTRIBUTION. Native of tropical Africa.

SPECIMENS:

WEST INDIES. TRINIDAD: cultivated in the Botanic Gardens (K).

41. **Combretum smeathmannii** Don, in *Trans. Linn. Soc. Lond.* xv: 425 (1827).

DISTRIBUTION. Native of western tropical Africa.

SPECIMENS:

WEST INDIES. CUBA: S. Clara, *Jack 8165* (NY).

SPECIES ERRONEOUSLY RECORDED FROM THE WESTERN HEMISPHERE

COMBRETUM VELUTINUM DC., *Prodr.* iii: 20 (1828). Based on a specimen supposedly from Brazil but now known to be African (see Aubréville, *Fl. Forest. Soud.-Guin.*: 116 (1950)). The species is the same as *C. molle* R. Br. ex Don (1827).

Species excluded from the genus

Combretum afzelii Hort. ex A. Juss. in Walp., *Rep. Bot. Syst.* v: 338 (1845–6) nom. synon. According to A. Jussieu (loc. cit.) *Hiraea houlletiana* A. Juss. was grown in English gardens under the name *Combretum afzelii.*

Combretum dipterum A. Rich., in Ramon de la Sagra, *Hist. Ile Cub. Bot.* i: 530 (1845), t. 43 (?) nom. synon. This name was given by A. Richard to a Cuban plant which he afterwards decided to describe as *Chicharronia intermedia* A. Rich. The name *Combretum dipterum* remained unchanged on the plate. Date of publication of the plate is obscure (see Urban, *Symb. Antill.* i: 143 (1898) for bibliographical notes). The plant is a species of *Terminalia.*

Combretum glaucocarpum Mart., in *Flora,* xxiv, Beibl. 2: 3 (1841). This is *Thiloa glaucocarpa* (Mart.) Eichl.

Combretum gracile Schott apud Spreng. in L., *Syst. Veg.* ed. 16, iv, App.: 406 (1827). This is *Thiloa gracilis* (Schott) Eichl.

Combretum nummularium Rusby in *Mem. Torrey Bot. Cl.* vi: 34 (1896). This is *Thiloa gracilis* (Schott) Eichl.

Combretum polyandrum Hoffmansegg ex Walp., *Rep. Bot. Syst.* ii: 6 (1843) nom. synon. According to Walpers (loc. cit.) this is *Moquilea paraensis* Mart. & Zucc.

Combretum stigmarium Mart., in *Flora,* xxiv, 1 Beibl. 2, 3 (1841). Based on plants growing in forests along the R. Amazon, Brazil. This is *Thiloa stigmaria* (Mart.) Eichl.

I am grateful to the Directors of the various institutions who lent me specimens and to those who allowed me to work in the herbaria in their charge. It is inevitable that ideas change during the course of a work of this nature, and they will find in their herbaria many specimens with identifications which differ from those given here and which I cannot now rectify personally.

I am also grateful to Miss D. Hillcoat for the illustrations made from my original pencil drawings.

Specimens cited listed under Collectors' Names

The number in **Clarendon** type after each specimen is that of the species in the systematic list to which it belongs (i.e. **25** means that the specimen is *Combretum laxum* Jacq.).

Aitken 1068, **13**. Akrinius? 648, **25**. Allen 352, **25**; 3432, **21**. Anderson 237, **13**; s.n. **21**. Anisits 2426, **6**; 2493, **6**. Appun 274, **13**; 288, **21**; 862, **25**; 1722, **25**. Archer 2373, **21**. Aublet s.n. **13, 21**. Baker s.n. **11**. Balansa 2336, **12**; 2337, **25**. Bang 1427, **12**; 1320, **17**. Barclay 9, **25**; 1994, **11**; s.n. **10, 11, 12**. Beauvois s.n. **25**. Beddington 10, **13**. Beechey s.n. **25**. Benoist 1511, **25**. Bernoulli & Cario 2979, **12**; 1981, **10**; 2982, **33**. Bertero 35, **12**. Blake 7847, **25**. Blanchard 193, **11**. Blanchet 9, **25**; 29, **12**; 726, **25**; 1517, **25**; 1549, **12**; 1558, **25**; 1717, **25**; 1759, **25**; 2115, **25**; 2172, **25**; 2720, **25**; 2759, **7**; 2866, **2**; 3105, **2**; 3107, **2**; 3261, **25**; s.n. **25**. Bolland 11, **12**. Bonpland 840, **13**; 1118, **34**; 3866, **25**; 3894, **11**; s.n. **21, 25**. Boon 1038, **22**; 1251, **13**; 1257, **21**. Boschwezen (Surinam) 1027, **13**; 1033, **25**; 2035, **21**; 2976, **25**; 3481, **25**; 3689, **13**; 5707, **25**. Botanic Gardens Herbarium (Trinidad) 1095, **12**; 2054, **12**; 3582, **12**. Bowie & Cunningham 422, **12**; s.n. **12**. Brenes 14529, **25**. Britton, Britton & Kemp 8, **38**. Britton, Freeman & Watts 2699, **12**. Britton & Mendelson 1586, **12**. Broadway 162, **12**; 6001, **12**; 7001, **39**; 7857, **12**; 10095, **39**; 10329, **12**. Brown 201, **12**; s.n. **12**. Burchell 2616, **25**; 2734, **25**; 6361, **25**; 6573, **7**; 6719, **1**; 6981, **1**; 6999, **1**; 7293–2, **1**; 7294, **25**; 7964, **19**; 8314, **6**; 8868, **19**; 9571, **24**; 9967, **25**; 10052, **13**. Calderon 355, **10**; 1431, **10**; 2130, **11**. Campbell 70, **12**. Carleton 481, **21**. Castellanos s.n. **12**. de Castelnau s.n. **13**. Chafer s.n. **12**. Chase 7807, **19**. Chaves 172, **11**. Clausen 72, **12**; 74, **7**; 75, **25**; 104, **25**; 106, **25**; s.n. **7, 25**. Conzatti 4378, **12**. Cook & Griggs 648, **25**. Crevaux s.n.

13. Crueger s.n. **12.** Dahlgren s.n. **19.** Dawe 76, **12**; 533, **25.** Deam s.n. **12.** De la Cruz 1374, **13**; 3425, **25**; 3585, **25**; 4104, **27**; 4129, **29**; 4460, **25**; 4528, **25.** Delport s.n. **25.** Herb. Desétang 48, **25.** Desvaux s.n. **22.** Herb. Desvaux s.n. **12.** Diquet s.n. **11.** Dodge & Allen 17501, **25.** Dodge, Steyermark & Allen 17981, **12.** Drouet, **25.** Duarte s.n. **6.** Duchassaing s.n. **12.** Dugaud & Garcia 2498, **12.** Dusen 11220, **12**; 11221, **12**; 15475, **12.** Eggers 1525, **25**; 2431, **25.** Ekman 1726, **25.** Elias 393, **12**; 609, **12**; 1073, **25**; 1328, **25**; 1350, **12**; 1354, **12.** Erlanson & Souviron 46, **11.** Fendler 282, **12**; 395, **12**; 2315, **34.** Ferris 5530, **12.** Fiebrig 4041, **6**; 4053, **8**; 4555, **6**; 5018, **12**; 5854, **12**; 5938, **12.** Focke 23, **21**; 355, **25**; 407, **13**; 832, **25**; 1416, **25**; s.n. **21, 25.** Forest Dep. (British Guiana) 3572, **21**; 3998, **13**; 4087, **13**; 4138, **25**; 5056, **24**; 5058, **27**; 6162, **25.** Forisell 169, **25.** Fox 97, **13**; 113, **13.** Friedrichsthal s.n. **11.** Funcke 310, **12**; 531, **12.** Galeotti 3051, **11.** Gardner 994, **25**; 1593, **6**; 1594, **19**; 1948, **12**; 2159, **2**; 2160, **2**; 2161, **8**; 2466, **12**; 2568, **25**; 3140, **25**; s.n. **8, 12.** Gaudichaud 1297, **12**; s.n. **12.** Gay s.n. **12**; Herb. Gay s.n. **12.** Geay 1903, **21**; 1904, **21**; 1905, **21.** Gentle 1285, **25**; 1881, **21**; 2388, **12**; 2600, **25**; 2700, **21**; 2753, **21.** Ghiesbreght 18, **11.** Glaziou 582, **6**; 587, **8**; 589, **25**; 3948, **25**; 3949, **12**; 7607, **25**; 8337, **12**; 8338, **25**; 8339, **25**; 8669, **25**; 9791, **13**; 9792, **8**; 9793, **2**; 10478, **7**; 10710, **6**; 10713, **5**; 10714, **8**; 10715, **19**; 10717, **25**; 10718, **5**; 10727, **17**; 11945, **15**; 12659, **12**; 13802, **24**; 13805, **12**; 13805*a*, **3**; 14687, **1**; 15325, **5**; 19143, **7**; 21122, **7.** Gleason 338, **27**; 397, **27.** Goldman 517, **12.** Gomez s.n. **25.** Goudot 1, **12**; s.n. **12.** Graham 174, **13**; s.n. **12.** Greenman 234, **11.** de Grosourdy 13, **9**; s.n. **34.** Guilding s.n. **34.** Hahn s.n. **11.** Halsted s.n. **12.** Hancock s.n. **11, 21.** Hart 7007, **39.** Hartweg 526, **10.** Hassler 1664, **12**; 5581, **12**; 5925, **12**; 6750, **12**; 7181, **19**; 7304, **25**; 7617, **8**; 8360, **12**; 8858, **12**; 10737, **2.** Haught 2250, **25**; 2275, **12.** Hayes 8, **21**; 31, **33**; 54, **25**; 308, **12**; 446, **12**; 541, **21**; 771, **25**; 783, **12**; s.n. **21, 25.** Heller 118, **11.** Heriberto 110, **21**; 214, **12**; 256, **12.** Herzog 186, **6.** Heyde & Lux 4173, **12.** Hinds s.n. **25.** Hinton 728, **12**; 3018, **33**; 3172, **33**; 3364, **11**; 3390, **33**; 5475, **33**; 5530, **11**; 5632 p.p. **11**; 5632 p.p. **12**; 9977, **11.** Holt & Blake 523, **25**; 658, **13**; 826, **9**; 853, **9.** Holton 924, **12.** Hostmann 138, **25**; 1032, **21**; 1153, **25**; s.n. **13, 25.** Hostmann & Kappler 825, **13**; 1153, **25.** Hulk 353, **13.** Isabelle s.n. **12.** Jack 8165, **41.** Jacquin s.n. **25.** Jellicoe 4096, **25.** Jenman 99, **25**; 355, **21**; 475, **13**; 737, **13**; 763, **21**; 1326, **21**; 2237, **25**; 3783, **25**; 4023, **25**; 4648, **25**; 4890, **21**; 4906, **25**; 5046, **13**; 5332, **25**; 5333, **21**; 5334, **25**; 6792, **22**; 6946, **12**; 7339, **25.** Johnson 1236, **21.** Jones 438, **25.** Jorgensen 2062, **25.** Jurado s.n. **12.** Jurgensen 174, **11.** Kappler 1828, **22**; 1998, **13.** Kegel 259, **25**; 1191, **21**; 1192, **13.** Kellerman 5648, **11.** Kickx s.n. **13, 25.** Killip 3295, **12.** Killip & Smith 14209, **12**; 14680, **25**; 23457, **12**; 23740, **12**; 26470, **12**; 26826, **16**; 27125, **25**; 29014, **12.** Kinloch 34, **12.** Klug 2237, **25**; 2608, **12**; 2780, **25**; 2785, **15**; 3130, **12**; 4118, **12**; 4325, **12.** Krukoff 1239, **19**; 1429, **13**; 2041, **8**; 4607, **25**; 4790, **25**; 4964, **25**; 5460, **25**; 5727, **25**; 6267, **25**; 6610, **25**; 8247, **25**; 8404, **25**; 8718, **25.** Kuylen s.n. **21.** Lalande s.n. **12.** Herb. Lamarck s.n. **21.** Lamb 468 p.p. **11.** Langlassé 9, **11**; 10, **11**; 129, **25**; 130, **25**; 461, **12**; 833 bis, **25.** Lanjouw 522, **25**; 701, **13**; 1158, **13.** Lankester K62, **11.** Le Blond s.n. **13, 14, 25.** Leeson s.n. **12.** Lehmann 2621, **12.** Lemmon 158, **12.** Le Moult 9, **21.** Leng 124, **25.** Leprieur s.n. **21, 25.** Leschenault s.n. **13.** Levy 329, **11**; 1291, **11.** Leybold 26, **11.** Liebmann 3410, **11**; 3418, **10.** Linden 1639, **12.** Lockhart s.n. **12, 25, 34.** Lorentz s.n. **12.** Lundell 2433, **12**; 2675, **25.** Luschnath s.n. **12.** von Lützelburg 442, **8**; 1386, **6.** Macedo 779, **12**; 1462, **7**; 1915, **25**; 2489, **25.** Maguire 23623, **21.** Maguire & Fanshawe 23355, **25.** Malme 1630, **12.** March s.n. **25.** Martin 59, **25**; 69, **25**; s.n. **25.** Martius 92, **12**; 115, **8**; 119, **25**; 410, **25**; 410 (7), **4**; 410 (8), **6**; 577, **8**; 578, **25.** Martyn 259, **13.** Matuda 3532, **35**; 3537, **25.** Maxon 4798, **21.** Maxon & Hay 3420, **11.** Mélinon 2, **25**; 45, **21**; 47, **22**; 69, **21**; 112, **22**; 251, **22**; 291, **25**; 296, **21**; 297, **13**; 308, **21**; 381, **21**; 444, **21**; 770, **25**; s.n. **13, 21, 22.** Mell 672, **12.** Menge s.n. **25.** Mexia 1130, **12**; 5979, **25.** Moloney 36, **12.** Montes & Salazar 118, **11.** Moricand s.n. **12, 25.** Moritz 1689, **34**; 1983, **12.** Morong 822, **25**; s.n. **12.** Mutis 1860, **12**; 3476, **12**; 3805, **12.** Myers 5705,

13. Nelson 2349, **12**; 2455, **25**; 3534, **12**; 6974, **11**. Nolte s.n. **13**. D'Orbigny 1017, **8**. Ørsted 3417, **10**. Ortega 105, **25**; 118, **11**; 4180, **11**; 4718, **12**; 5201, **11**; 5625, **11**; 5676, **11**; 6792, **11**. Page s.n. **19**. Palmer 377, **25**; 396, **33**; 397, **11**; 1067, **11**; 1374, **25**. Parker s.n. **13**, **25**. Pavon s.n. **12**, **25**, **36**. Peck 344, **12**; 744, **25**; 880, **25**. Pennell 3772, **16**; 4018, **12**; 4138, **12**. Pennington s.n. **12**. Perez 524, **12**. Perrottet s.n. **13**, **14**. Philipson, Idrobo & Fernandez 1630, **25**. Pickel 137, **25**; 143, **6**; 2750, **12**. Piper 5489, **12**. Pittier 1784, **10**; 2158, **12**; 2692, **21**; 4002, **34**; 4169, **25**; 5006, **12**; 5548, **16**; 6607, **33**; 6668, **25**; 6810, **25**; 7659, **12**; 8168, **12**; 8726, **12**; 8761, **12**; 9901, **12**; 10161, **12**; 10652, **12**; 11691, **34**; 12013 p.p. **11**; 12084, **12**; 12140, **11**; 13304, **12**; 14545, **12**. Plée s.n. **34**. Poeppig 1898, **12**; 2493, **24**; 2494, **30**; s.n. **24**, **30**. Pohl 1096, **2**; 1484, **25**; s.n. **19**. Poiteau 641, **25**; s.n. **21**, **25**. Pollard 58, **13**. Popenoe 958, **11**. Pringle 8371, **12**. Pulle 442, **13**. Purdie s.n. **9**, **12**, **13**, **34**. Purpus 360, **11**; 8637, **11**; 14002, **11**; 14203, **11**. Quiroga s.n. **12**. Rech 76, **22**. Record s.n. **12**. Regnell s.n. **12**. Reko 3523, **10**; 3750, **10**; 4916, **33**; 5106, **33**. Renson 36, **12**; 68, **12**. Richard s.n. **12**, **13**, **14**, **21**, **25**, **27**. Herb. Richard s.n. **34**. Ridley, Lea & Ramage 59, **32**. Riedel 24 p.p. **19**; 24 p.p. **25**; 406, **25**; 530, **12**; 752, **1**; 862, **7**; 1759, **12**; 2050, **12**; in Herb. Hance 5748, **25**; s.n. **19**, **25**. Riedlé 38, **12**; s.n. **34**. Robert 390, **3**; 390*b*, **3**; 595, **3**; 743, **8**. Robertson 222, **21**; 288, **25**. Rodriguez 316, **12**; 316*a*, **12**. von Rohr 43, **12**; 149, **14**; 435, **27**; s.n. **34**. Rose 1416, **11**; 14185, **11**; 21836, **12**. Rose, Painter & Rose 9414, **12**. Rose, Standley & Russell 13107, **11**; 13849, **11**; 14185, **11**; 14510, **11**. Rosengurtt B1066, **12**. Rovirosa 206, **35**; 612, **35**; 2349, **12**. Ruano 873, **10**. Ruiz s.n. **12**. Rusby 623, **17**; 721, **25**; 1773, **13**. Rusby & Squires 265, **13**. Sagot 1, **25**; 241, **25**; 242, **21**; 255, **25**; 849, **13**; 944, **22**. St-Hilaire 62, **12**; 735, **12**; 754, **12**; 1325, **12**; 1844, **25**; s.n. **12**. Salas 646, **11**. Sandwith 619, **21**; 628, **13**; 1551, **25**. Sargent 10, **12**. Schipp 36, **12**; 42, **12**; 87, **21**; 356, **25**; 768, **25**. Schlim 279, **12**. Schomburgk 33, **21**; 55, **22**; 87, **12**; 106, **25**; 272, **21**; 509, **25**; 758, **21**; 871, **27**; 872, **25**; 1480, **25**. Schramm 5, **12**. Schultes 5452, **9**; 5501, **13**. Seeman 614, **33**; 1658, **25**; 6141, **33**; s.n. **12**. Seler 3311, **33**; 3325, **10**. Sello 443, **25**; s.n. **12**, **15**. Shannon 5038, **11**; 5039, **10**. Sinclair s.n. **10**, **11**. Skinner s.n. **11**. Smart Axxxi, **12**. A. C. Smith 2377, **13**; 2493, **13**; 2566, **25**; 2595, **25**; 2689, **22**; 3019, **25**; 3105, **13**. C. L. Smith 11, **21**. D. Smith 144, **19**. H. H. Smith 874, **12**; 883, **25**; 885, **25**; 1947, **25**; 1948, **25**; 2101, **33**. J. D. Smith 1646, **21**; 1707, **25**; 6230, **10**. Splitgerber 109, **21**; 112, **13**; 334, **21**; 829, **13**. 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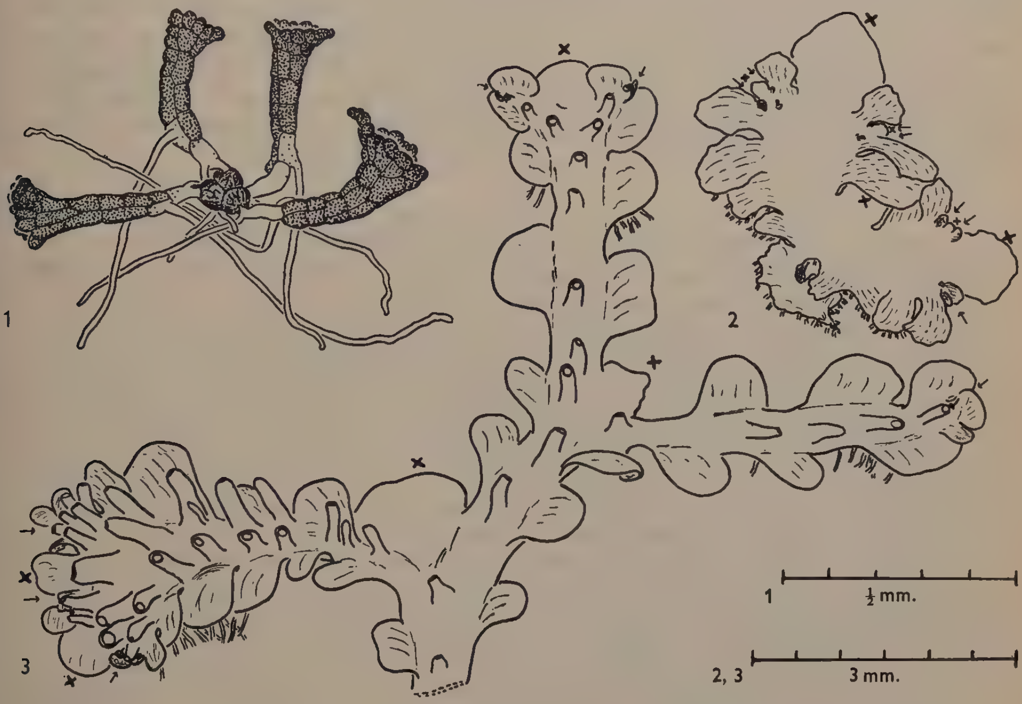
On Sphaerocarpos stipitatus and the genus Sphaerocarpos.

By JOHANNES PROSKAUER, University of California, Berkeley

(With Plates 14 and 15, containing Figs. 43–50, and 42 Text-figures)

[Read 19 November 1953]

The genus *Sphaerocarpos* is pre-Linnean, having been established by Micheli in 1729. Its validation stems from the description by Boehmer (in Ludwig, 1760).[1] The gametophyte (Figs. 2, 3) has an axis which forks repeatedly and bears two rows of alternately arranged appendages. These 'leaves', in the terms of the bryologist, show a 'succubous' insertion, that is, they are inserted obliquely with the posterior part of one leaf tending to lie above the anterior margin of the leaf just behind it. A very prominent additional feature is the possession of large middle lobes or 'angle leaves' (marked by an × in the figures) subtending the dichotomies. The fact that *Sphaerocarpos* is 'leafy' has been repeatedly pointed out, only to fall into partial oblivion (e.g. Campbell, 1896*a*; cf. Douin,



Figs. 1–3. *Sphaerocarpos stipitatus.* Fig. 1. Sporelings from one tetrad, grown on agar. Fig. 2. Young female plant, grown on agar. The first archegonia just formed. Juvenile thallus still attached. *S. cristatus* or *texanus.* Fig. 3. Female plant grown on moist soil. Archegonia not fertilized. × =middle lobe; ↑ marks growing point.

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[1] In the text of the validating work the original spelling *Sphaerocarpos* was used; in the index the latinized variant *Sphaerocarpus* occurs, probably the result of a misprint. This latter spelling has been adopted by a majority of subsequent authors. There is no merit in it (cf. Haynes, 1910; and the current International Code, Article 82). Fortunately no attempt has been made to latinize *Anthoceros*, another generic name of Greek derivation coined by Micheli at the same time. Micheli gave the name *Sphaerocarpos* explicitly in reference to the round capsule, not the protecting structures.

1930). If one scans the text-book and floristic treatments of the genus one finds that a legend, savouring of medieval herbal lore, exists which interprets the thallus of *Sphaerocarpos* as having the form of a cordate fern prothallus. This even resulted in the establishment of Lotsy's (1909, p. 88) hypothetical 'Sphaeroriccia', based on the combination of the allegedly simplest gametophyte with the simplest sporophyte. The earliest accurate drawings of *Sphaerocarpos* appear to be those by Bischoff (1827).

The present study owes its origin to Dr M. A. Pocock, who very kindly supplied both living and preserved material of a South African member of the genus *Sphaerocarpos*. It appeared markedly different from the commonly studied species of the Northern Hemisphere. In 1829 Bertero collected near Valparaíso, Chile, a *Sphaerocarpos* which was described both by Lindenberg (1837) and Montagne (1838) as a new species. Their incomplete descriptions, augmented by that given by Haynes (1910), suggested to me that this plant might have some connexion with the African one. A more detailed examination of the Chilean plant was requisite. As far as I know it has never been collected since Bertero found it. In July 1949 I searched for it in vain in the Valparaíso area. I am greatly indebted to Dr S. Jovet-Ast for locating in the Muséum National d'Histoire Naturelle, Paris, several packets of the original collection. These, together with a further one from the Royal Botanic Gardens at Kew, were kindly lent to me. Their study revealed that the South African and Chilean plants appear indeed to be representative of the same species, *S. stipitatus* Bischoff ex Lindenberg.

SPHAEROCARPOS STIPITATUS: BERTERO'S MATERIAL FROM CHILE

To help in the disentanglement of various discrepancies in the literature, brief accounts of the packets available to me are here given:

a. (Montagne Herbarium, Paris.) 'Sphaerocarpus Berterii Montg. Chili. Bertero.' A fragment of a single female thallus, dried on mica. Only immature sporophytes.

b. (Herb. Paris.) 'Sphaerocarpus Berterii Montg. et S. terrestris mixti. Sphaerocarpus chilensis. Quillota. Ex Bertero No. 695', written in the hand of Montagne. Inside is a further label: 'Sphaerocarpus Michelii in pascuis humidis coll. Quillota (Chile) 1829 jul.', possibly written by Bertero. The specimens are on paper labelled '695' (665?) 'Sphaerocarp terrestris'. They appear to be a form of *S. texanus* Austin. A fragment of *S. stipitatus* is glued on another piece of paper.

c. (Herb. Paris.) 'Sphaerocarpus stipitatus Bischoff in litt. Sph. terrestris Bertero nr. 1331. ad fossarum margines. Quillota. Chile' 'Herbarium Steudel.' Later marked 'type' by F. Camus. It contains some material of *S. texanus* and several fragments of *S. stipitatus*. From one of the latter some fairly mature spores were obtained.

d. (Herb. Kew.) 'Sphaerocarpus chilensis Mont. olim. S. Berterii Mont. Centurie. S. stipitatus Bischoff. Chili', written by Montagne. One female *S. stipitatus* and, glued on separately, one fragment with more or less mature spores.

e. (Montagne Herb., Paris.) 'Sphaerocarpus Berterii Montag. S. stipitatus Bisch. Quillota legit Bertero.' Two patches, both of *S. stipitatus*. No ripe spores.

f. (Herb. Paris.) 'Sphaerocarpus Michelii Bell.—terrestris Engl. Bot. Chili. Bertero.' Eight patches, all *S. stipitatus*. No ripe spores. Some male plants.

g. (Montagne Herb., Paris.) 'Nees No. 98. Riccia ochrospora N. et M. adapté par M. Lindenberg.' Isotype of *Riccia ochrospora* associated with some fragments of *S. stipitatus*.

The description and figures by Lindenberg (1837) are based on a packet of Bertero Nr. 1331 (i.e. the same number as packet *c*) from the Hochstetter herbarium. From this Lindenberg adopted the manuscript name '*Sphaerocarpus stipitatus* Bischoff'. His descriptions are incomplete in so far as he did not mention the male plants, and stated that no ripe spores could be found.

The name '*Sphaerocarpus Berterii* Montagne' (1838) is based on Bertero Nr. 695 (i.e. packet *b*, and probably some of the others). Montagne stated that the plant occurs, together with *Riccia ochrospora*, as packet *g* verifies. The diagnosis is rather brief, and the spores are described as 'tricoccis, subasperis'. Essentially the same description is repeated in Montagne 1850 and 1856, and also in Gottsche, Lindenberg, and Nees, 1844. However, in 1839, Montagne published an extended diagnosis, in which he described the spores as: 'Tricoccae, subasperae, subaurantiacae, e membrana grosse arcolata endogonium fingente, demum evanescente, oriundae, in peripheria cellulis ad speciem articulatis marginatae.'[1] This description nonplussed me for some time, until I arrived at the following explanation. Nees v. Esenbeck (1838), for no apparent reason, included the Chilean plant in his treatise on European liverworts. He examined the material in the Hochstetter herbarium, which he stated had been collected near Quillota in August and September 1829.[2] The first part of his description certainly refers to *S. stipitatus*, but he made the following observations concerning the spores: 'Die Samen sind pomeranzengelb. . . . Die zellige Samenhaut bildet im Umfange einen gegliederten Ring.' The last sentence can only refer to the spores of *S. texanus*, found also in Bertero Nr. 1331, cf. packet *c*. As his references show, Montagne had this account already available in 1839. His revised description of the spores becomes intelligible as a blend of his own previous one, and the erroneous one by Nees v. Esenbeck.

Stephani (1899), who changed the spelling of the name given by Montagne to '*Sphaerocarpus Berteroi*', supplied additional details about the anatomy of the plant. He was the first to mention the male thalli. Miss Haynes (1910) examined a specimen from the Paris Museum and prepared some drawings illustrating morphological features. She did not see mature sporophytes.[3]

Although the material of *S. stipitatus* from Chile, available to me, appears rather uniform, the following description is based where possible on material from packet *c*, as this is part of the collection on which Lindenberg made the original study.

In the dried material *S. stipitatus* can be distinguished at first sight from *S. texanus* by the lighter brown colour of the former. Most of the specimens of *S. stipitatus* are female thalli, showing but relatively early stages in the development of the sporophytes. The vegetative parts of the female gametophyte basically conform to the structure normal in the genus, showing a much branched axis bearing 'leaves' and middle lobes a single layer of cells thick. Their striking feature is the fact that the 'bottles'[4] containing the archegonia become elevated on stalks which continue to elongate during their development (Figs. 14, 43). In no other species of this genus does such a stalk exist. Thence the apt epithet '*stipitatus*'. The longest stalk seen measured *ca.* 1·5 mm. A second feature of the bottles not shared by other species is that their walls consist of two layers of cells, rather than one. Lindenberg already remarked that the wall was multilayered, and Stephani (1899) and Haynes (1910, pl. 32, fig. 3) supplied some additional details. Fig. 26 shows the top part of the wall of a bottle, which had been more or less bisected longitudinally, as seen from the inside. The mouth of the bottle is surrounded by a single ring of large cells, below them the inside is lined by cells with teat-like outgrowths. These teats are curved downwards. Staining with iodine revealed dense granular starchy contents in the cells of this layer, whilst the cells of the outer layer proved nearly empty. The inner layer is reminiscent of the roof to the assimilatory chambers of *Cyathodium* (Proskauer, 1951, fig. 5).

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[1] Bravely rendered by Miss Haynes (1910) as: 'the persistent spore-tetrads yellowish, coarsely areolate and somewhat roughened, marginate'. This makes it clear that she too was at a loss to understand it and assumed misprints.

[2] This would date Bertero Nr. 1331, packet *c*, as opposed to Nr. 695, packet *b*, which was collected July 1829.

[3] Her description of the specimen: 'B. Bertero, 695, August and September 1829' was probably taken from the literature rather than the packet, and is surely incorrect. Cf. preceding footnote.

[4] = 'ampullae' of Micheli (1729) and Boehmer (1760). These integument-like structures have been called 'involucres' by most of those recent authors who have tried to give them a technical name. In *Marchantia* the corresponding structure is termed 'perianth' or 'pseudoperianth', and the term 'involucre' reserved for the larger flaps ('perichaetium'). The antiquated unsuitable term (cf. Goebel, 1930, p. 858) 'perianth' was used by Goebel (1930, p. 817) and Lindenberg (1837) also in reference to *Sphaerocarpos*.

The contents of two capsules in a fairly advanced stage of development, found among the fragments in packet *c*, were examined. In addition, a few tetrads were obtained from packet *d*. The spores remain permanently united in tetrads, as in most other species of the genus. The tetrads from the three capsules were fairly uniform in appearance. They were golden brown and gave the impression of not being fully mature. The ridges on the surface of the spores present a characteristic system; rather than attempting a verbal description, reference is made to Fig. 28. The only other species which has markings of the same basic pattern is the little known *S. drewei* Wigglesworth (1929) from Southern California. A tetrad from isotype material of the latter (in Herb. Univ. Calif.) is shown in Fig. 34. In this species the ridges are continuous from spore to spore, whereas in *S. stipitatus* they are less massive and their development stops short at the edges of the individual spores. Occasional tetrads of *S. hians* Haynes and individual spores of *S. cristatus* Howe may approximate this pattern also (cf. figures in Haynes, 1910). Neither the structure of the capsule wall, nor the sterile cells, could be made out with certainty in the Chilean specimens of *S. stipitatus*.

A few male plants were found in intimate association with female plants of *S. stipitatus* in packet *f*. As this sample contains no female thalli of *S. texanus* these males can be presumed to belong to *S. stipitatus*. As usual, they are much smaller than the female plants (Figs. 15, 43). They show the normal 'leafy' thallus, and the bottles containing the antheridia are neither stalked, nor do they show a second layer of cells on their insides. Some of them show the usual deep red colouring, especially in the older bottles.

SPHAEROCARPOS STIPITATUS: SOUTH AFRICAN MATERIAL

Origin of material. All the material was gathered by Dr M. A. Pocock at the only locality so far known, viz. muddy banks of pools in the Palmiet River (tributary of the New Year's River), on the Cradock Road, 7 miles from Grahamstown, Cape Province, South Africa. Dr Pocock informed me that it was originally found there by Miss Lilian Britten of Rhodes University College. The Palmiet River only runs after rain; at other times the bed harbours a series of deepish pools with overhanging banks. According to Dr Pocock the *Sphaerocarpos* grows on the shady north banks, protected by other vegetation. The normal months of its development are August and September; it disappears when the banks dry up. As is usual for the genus, it is associated with species of *Riccia*. Preserved material available to me was collected in September of 1944 and 1951 respectively. The cultures were prepared from spores of dried material dated 2 September 1951.

Germination and sporelings. Tetrads were sown on an agar medium.[1] The cultures that are described here were started at Berkeley, California, in October 1952. Germination occurred within about 10 days. The great majority of the 13-month-old tetrads germinated perfectly, and this proved true of tetrads of all sizes and range in colour from yellow brown to blackish (see below). The largest blackish tetrads lagged behind somewhat. After the establishment of plants, transfers were made to loam in culture dishes.

In most instances each of the four spores of a tetrad gave rise to a sporeling. The spore ruptures on its only free face, the outer one. A tetrad with its four sporelings is shown in Fig. 1. The first stages in the development conform to what will probably in due course become recognized as the basic land plant gametophyte pattern: a radial upright obconical structure is formed, which acquires a depression at the top. This depression is completely surrounded by a flange of tissue one layer of cells in thickness. An apical growing point becomes established on one side of this flange. Its activity results in the development of a tongue of tissue one layer of cells thick, which grows more or less

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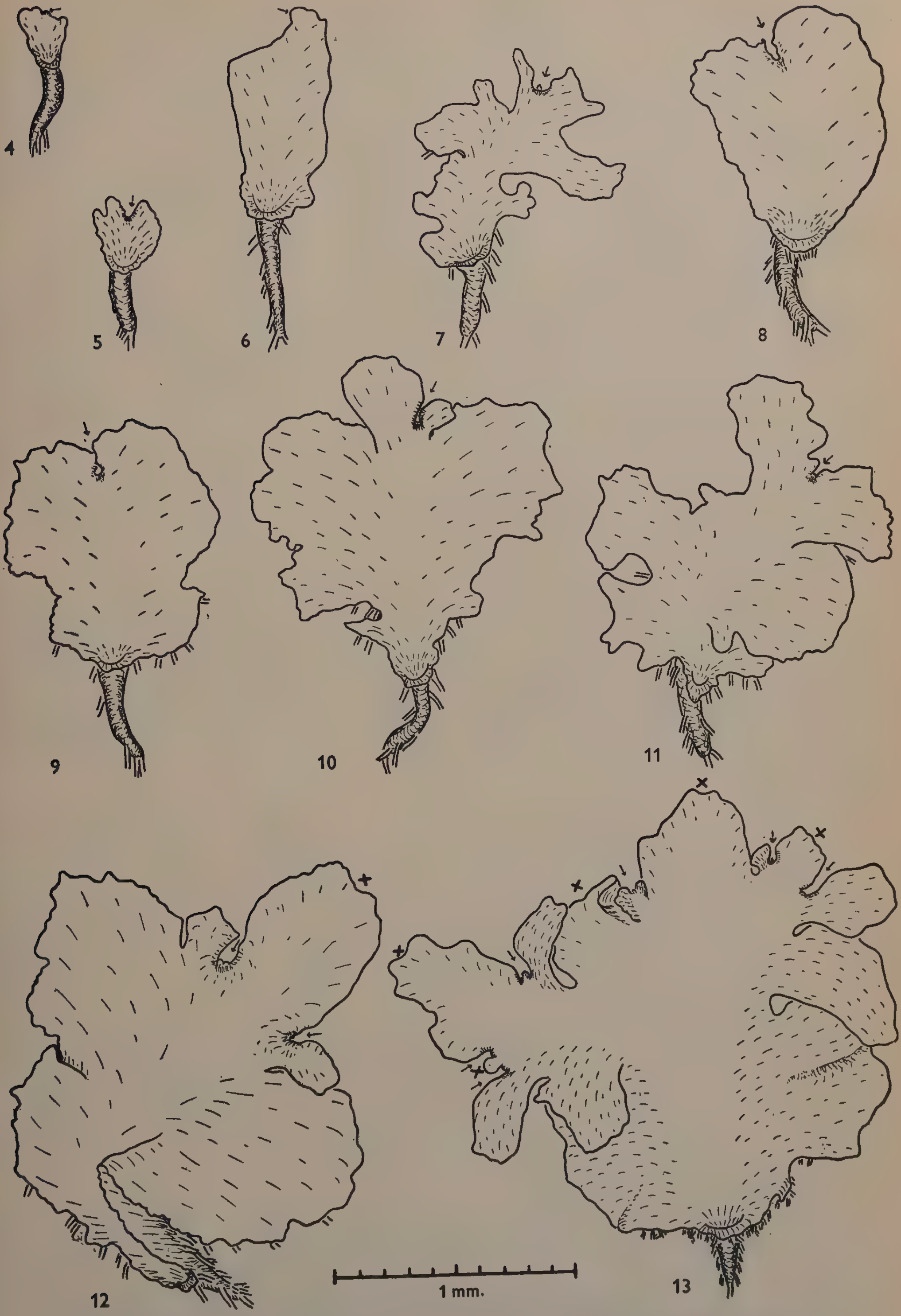
[1] 0·2 g. NH_4NO_3; 0·1 g. each of $CaCl_2$, KH_2PO_4, $MgSO_4$; 0·005 g. $FeCl_3.6H_2O$; 15 g. agar; 1 l. distilled water.



Figs. 4–13. *S. stipitatus.* Stages in the development of sporelings through juvenile to beginning of adult phase. (Agar culture.)

horizontally and forms the beginning of the juvenile thallus (Figs. 4, 6). This juvenile thallus usually becomes cordate, with the growing point lying in an apical notch (Figs. 5, 8 and 9). This is as close as *Sphaerocarpos* ever comes to the cordate fern prothallus type of structure with which it has been credited by some. That there is the usual degree of plasticity is attested by Figs. 7 and 11. As in other species, multicellular ventral hairs protect the growing point. In most specimens in my cultures the first two 'leaves' had differentiated before the first dichotomy became apparent (Fig. 10). In the angle of the dichotomy arises the first middle lobe (×, Fig. 12). Further development is on the typical adult plan, with an axis which forks repeatedly and bears leaves and middle lobes (Fig. 13). In this species I have never seen specimens which are as jungermannioid as that shown in Fig. 3, although all examined conformed to the same basic pattern.

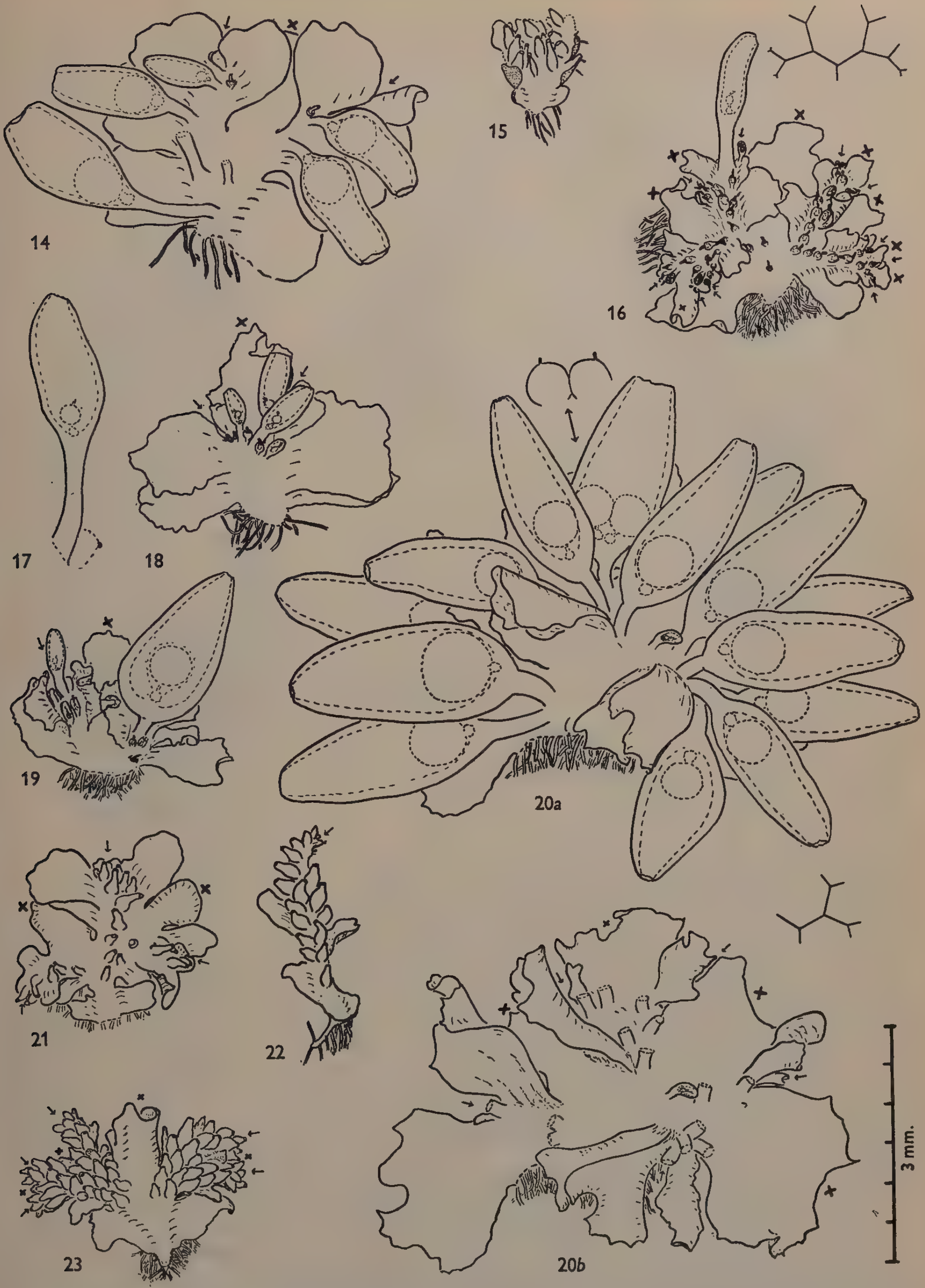
In my cultures the first sex organs made their appearance at the beginning of the adult phase in the male plants. The female plants lagged behind in this respect and only formed archegonia after a limited phase of sterile adult development (Fig. 2). The first mature sex organs were seen towards the middle of January. The earliest formed sex organs of a thallus in some instances failed to develop properly, as has been observed by Allen (1937) and Heitz (1943) in *S. donnellii*. Male and female plants could not be distinguished at sight from one another before the formation of the sex organs. Their ultimate difference in size results from later growth, a state of affairs comparable to that found in *Phaeoceros laevis* (Proskauer, 1948, p. 249). I believe that in both instances the smaller size of the male plants is predominantly due to the fact that they produce antheridia to the limit of their capacity, rather than to cytological causes of the nuclear-volume–cell-volume ratio type.

Adult male plants. Figs. 22 and 23 show somewhat attenuate and normal broad male plants respectively; in both instances the juvenile thallus is still attached. Both specimens were collected in the field by Dr Pocock. The male plants in the cultures are usually more luxuriant; in proportion they show a greater development of the vegetative parts and less crowding of the bottles (Fig. 21). This condition should, however, not be called abnormal. Similar luxuriant specimens belonging to the local Californian species can generally be found without much difficulty in the field, where they owe their origin to especially favourable microclimatic factors.

I know of no morphological feature which differentiates the male plants of *S. stipitatus* from those of other species of the genus.

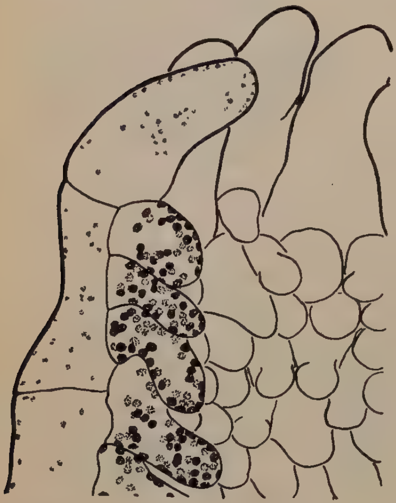
Adult female plants. Figs. 16, 18 and 19 show fragments of female thalli collected in the field. They all show the normal pattern of development of the vegetative parts. It is possible to see this, because the archegonia were either not fertilized, or had only reached the earlier stages of pregnancy. Fig. 20*a* shows a fragment of a female rosette covered with bottles containing more or less mature sporophytes. It is in this condition that *Sphaerocarpos* is usually gathered for deposition in herbaria. The large size and great number of the bottles tend to hide the vegetative parts of the thallus. To examine them, two methods exist: either one can turn the thallus upside down and clean off the soil and rhizoids, or one removes the bottles. The latter operation was performed on the fragment shown in Fig. 20*a* (Fig. 20*b*). It is evident that even here the thallus bears appendages. The plan of the branching accompanying the figure may help to illuminate the confusing picture. The confusion is due to enlargement and displacement of parts concomitant with increase in size of the bottles.

The bottles. Whereas in the male plants the bottles are sessile and have a wall composed of a single layer of cells, thus agreeing with those of other species of *Sphaerocarpos*, in the female plants the bottles are stalked and have a double-layered wall. The two cell layers are apparent already at an early stage of development (Fig. 24). Only at the mouth of the bottle is there a ring of single cells. This ring ultimately becomes alined with the outer layer of cells and forms the teeth around the orifice. As development proceeds, the cells of the inner layer become more numerous than the cells of the outer one. They



Figs. 14–23. *S. stipitatus*. Material from Chile, leg. Bertero: Fig. 14. Fragment of female plant with immature sporophytes. Some of the damaged leaves drawn reconstructed. Fig. 15. Small male plant. Material from South Africa: Figs. 16–20. Fragments of female plants (preserved). Figs. 20*a* and *b* show same fragment before and after removal of bottles. Fig. 21. Fragment of male plant (agar culture). Figs. 22, 23. Male plants from preserved field material. × = middle lobe; ↑ marks growing point.

are smaller, have denser contents, and produce teat-like outgrowths. These are larger in the upper part of the bottle than in the lower region, where the inner layer is often partially destroyed (Figs. 46–48). Fig. 25 shows part of the apical portion of a bottle which had been split open longitudinally, seen from the inside. The chloroplasts in the large cells of the outer layer, as well as those of the ring of cells around the mouth,



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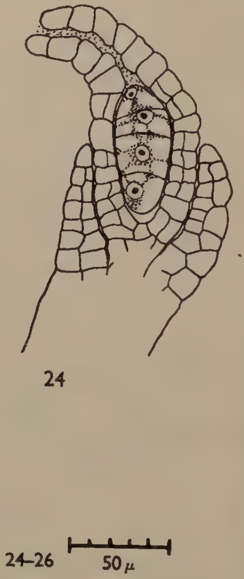

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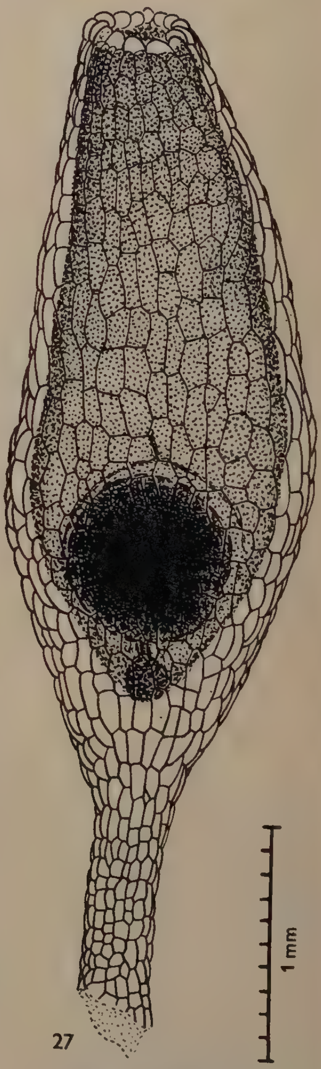

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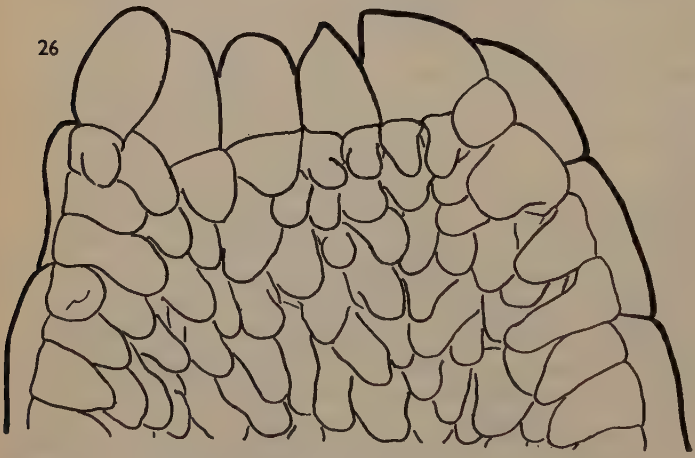

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Figs. 24–27. *S. stipitatus*. Fig. 24. Archegonium with four-celled embryo; developing bottle. (Optical section of stained whole mount.) Figs. 25, 26. Mouth region of mature bottles split open lengthwise, as seen from inside. Plastids omitted in most cells. Fig. 27. Bottle with nearly mature sporophyte. Fig. 26 from isotype material, the rest from material preserved in South Africa.

gradually degenerate. The inner layer is highly photosynthetic and accumulates considerable amounts of starch. The plastids are especially crowded in the teats. Seen from the outside, the large cells of the outer layer form a translucent mantle around the densely green lining (Fig. 27).

When initiated, the bottles are sessile structures. The stalks develop by intercalary activity. The longest one seen in preserved material from South Africa measured *ca.* 1½ mm. (Fig. 17), most are from ½ to 1 mm. in length. They are usually some six cells wide in section. Their cells show no particular specialization.

The bottles arise as integument-like outgrowths around the bases of individual archegonia. However, one instance was observed of two sporophytes having developed within a common bottle. Dissection revealed the presence of two archegonial necks on separate calyptrae (Fig. 20*a*), and in this instance two archegonia were therefore present (cf. Rickett, 1923, p. 233). Similarly, I observed one case of two antheridia sharing one bottle.

Sporophytes. The structure and development of the sporophyte conform to the pattern described for other species of the genus by previous authors (e.g. Leitgeb, 1879; Campbell, 1918; Goebel, 1930). Fig. 24 shows an embryo at the stage of the four-celled filament. In the one represented in Fig. 47 the differentiation into capsule, seta, and foot has occurred. The foot never penetrates the tissue below the original archegonium. It is very rich in chlorophyll, even in mature sporophytes.[1] The seta is composed of four rows of cells. It becomes necrosed well before the capsule reaches maturity (cf. Fig. 46). This disturbing phenomenon was observed also in other species by the three authors listed above. In these other species the calyptra soon breaks down and disappears, so that the capsule is held in position by the dead seta only. In *S. stipitatus*, however, the calyptra remains unruptured and crowned by the persistent archegonial neck even at the time the capsule has fully matured (cf. Fig. 20*a*). The large flat cells of the calyptra then still contain a nucleus and a few degenerating plastids. This persistence of the calyptra I have observed also in the Californian *S. cristatus*, in which species it has, indirectly, been used as a taxonomic character, as will be discussed later in this paper.

The capsule is composed of a jacket a single layer of cells in thickness, surrounding a central tissue which ultimately gives rise to spore mother cells and the so-called 'sterile cells'. Both jacket and sterile cells contain chloroplasts and are normally crowded with starch grains. It is probable that after the death of the seta the tetrads benefit from this. As in other species, at one stage of development the contents of the capsule shrink away from the jacket; later the tetrads and sterile cells are again evenly distributed in the cavity (cf. Figs. 46 and 48).

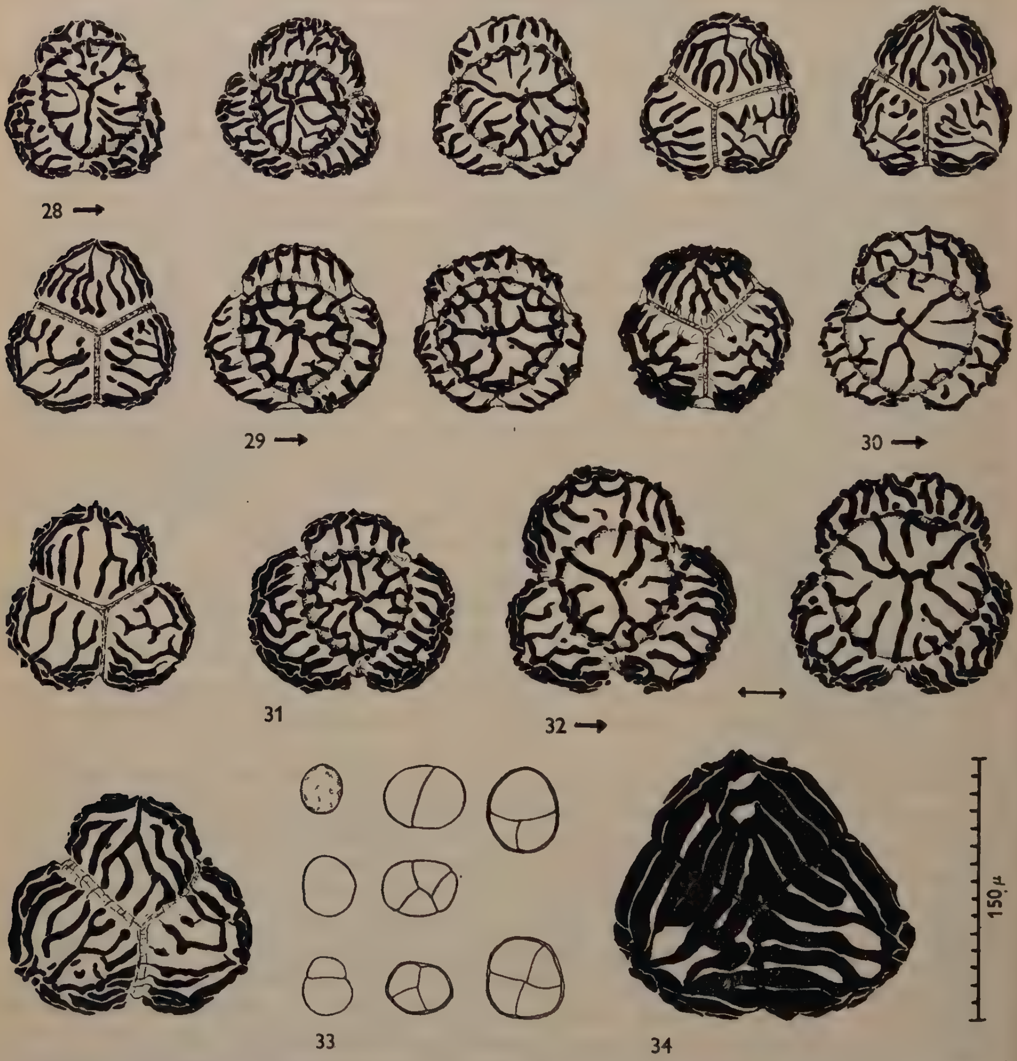
'*Sterile cells.*' In common with almost all other liverworts, the sporogenous tissue becomes differentiated into spore mother cells and sterile cell initials. The situation in *Sphaerocarpos* is remarkable in so far as these two cell types here have greater similarity in their further development than in any other known case. In both, the original nucleus usually undergoes two successive divisions, resulting in four nuclei, but whereas in the spore mother cells the divisions are meiotic, in the sterile cells they are normal mitoses, and the nuclei therefore remain diploid. The whole subject was reviewed and expanded by Gross & Allen (1938) in a study of *S. donnellii*. In *S. stipitatus* the basic phenomena are the same. But Gross & Allen reported that in *S. donnellii* the cell plates formed on the spindles during the mitoses disappear, without apparently giving rise to partition walls.[2] They remarked that observations on this point are somewhat difficult, mainly because of the abundant starch and plastids, which holds true also for *S. stipitatus*. Here it seems that sometimes the cell plates disappear, whereas they persist in other instances. Thus, at maturity the resulting structure may be composed of from one to four cells. In some instances there appeared to be a distinct membrane surrounding the whole group, thus further enhancing the resemblance to the fertile cells (Fig. 33). Four nuclei are present in almost all instances, whether cell walls are formed or not. Six or eight nuclei were seen in a few sterile cells in microtome sections, but no entire units with more than four cells were observed.

Spores. Figs. 29–32 represent tetrads taken from four separate capsules of *S. stipitatus* collected in South Africa. Within each capsule all tetrads are more or less of the same

[1] Cf. also Studhalter, 1942.

[2] But see Siler, 1934, footnote on p. 568.

size and colour. There may be, however, a marked difference in size of tetrads taken from different sporophytes. The largest tetrads have a maximum diameter of *ca.* 135μ, the majority measure *ca.* 110μ, and the lower limit lies around 95μ. One of the larger tetrads has roughly 2½ times the volume of one of the smaller ones. The colour of the tetrads varies from pale yellow brown through brown to almost black, but these colours could be found associated with tetrads of all sizes. The tetrads with black colouring were found in the oldest sporophytes of individual thalli, presumably if given the time all tetrads would become black. From an examination of immature capsules I am led to conclude that there is no further growth once the spore coats are being organized, which happens simultaneously in all the tetrads of a capsule. The size difference appears to be a function of different nutritive conditions within individual sporogonia, although the



Figs. 28–34. *S. stipitatus.* Isotype material. Fig. 28. Tetrads. Material preserved in South Africa. Figs. 29–32. Tetrads. The first two drawings of Fig. 32 show the same tetrad in different views. Fig. 33. Sterile cells from mature capsules. Plastids omitted in all but one. *S. drewei.* Isotype material. Fig. 34. Tetrad. Tetrads listed under the same number are from same capsule.

detailed factors are not yet fully understood. The size of the capsules varies greatly, as does the number of tetrads which they contain. A sample count yielded *ca.* 82 tetrads in a small capsule, and *ca.* 295 in a very large one. In both instances the tetrads were of average size. A similar variation in size of tetrads is known to exist in *S. texanus*.

Because of the diversity in colour and size the question of what constitutes a 'mature' tetrad arises. As stated above, tetrads representing the whole range of variation, from dried material gathered 13 months earlier, were sown on agar. Most of the tetrads germinated, and this was true of some of all kinds. From this point of view, then, a tetrad is mature when the spore coats are fully formed, notwithstanding any subsequent change in pigmentation. It remains to investigate the longevity of the tetrads over a span of years.

If the spores of individual tetrads are examined it appears that there are usually a smaller and a larger pair. The first two drawings of Fig. 32 show this in a tetrad seen from two aspects; usually the size difference is not quite so extreme. It may be that the smaller pair gives rise to the male plants, and the larger to the female, but I have no experimental evidence in support of this, although it has been demonstrated to be true in *S. donnellii* (Lorbeer, 1934). The sporelings from the spores of various sizes, and, for that matter, from tetrads of various sizes, are roughly of the same dimensions (cf. Fig. 1).

A comparison of Figs. 28–32 shows that the tetrads of the type material of *S. stipitatus* (Fig. 28) fall into the range of variation of the much more abundant South African material, especially if it is borne in mind that the former were probably not yet fully formed at the time they were collected.

The discharge of the spores is by decay of the surrounding tissues. In this species it is the capsule wall which disintegrates first. The tetrads then lie loose in the calyptra, which still is crowned by the archegonial neck.

Cytology. The following observations on chromosomes are based on aceto-carmine squash preparations made in the way outlined in Proskauer (1948). The material was taken from the cultures described above; male and female plants were identified as such by their sex organs.

Both male and female plants have a chromosome complement of seven autosomes and one sex chromosome. In the male plants the sex chromosome is minute and considerably smaller than any of the autosomes (Figs. 35–38, 49). The female sex chromosome, on the other hand, is very much larger than any of the autosomes (Figs. 39–42, 50). Both sex chromosomes are heterochromatic, as is shown by prophase stages (Figs. 35, 39). In these prophases the nucleolus proved very difficult to stain.

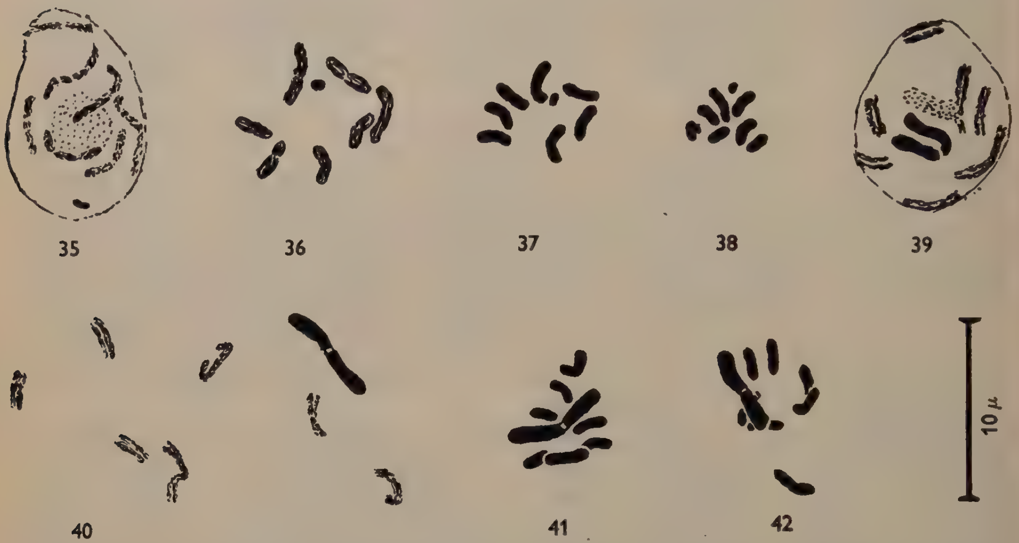
The study of the cytology has been confined to the haploid mitosis, because so far no suitable sporophytic material has become available from the cultures.

A similar remarkable difference in size between the male and female sex chromosomes has previously been demonstrated in *S. donnellii*, *S. michelii*, and *S. texanus* (cf. Allen, 1919; Lorbeer, 1934). In *S. cristatus* the difference between the two is much less (Allen, 1936), just as it is in the dioecious species of the allied genus *Riella* which have been investigated (Lorbeer (1934), on *R. helicophylla*; own unpublished observations on *R. purpureospora*).

The genus *Sphaerocarpos*

As explained earlier, it is erroneous to regard the 'leafy' form of the thallus of *Sphaerocarpos* as an exceptional rather than the normal development, and it appears to be so in both male and female plants of all described species. In the adult female plants the vegetative part of the thallus tends to be hidden by the large bottles, but can be revealed by their removal. Only in the juvenile condition is there a cordate thallus. The male plants may sometimes begin the formation of antheridia in the juvenile stage. Such specimens can occasionally be found in the field in the California species, and one has been figured by Campbell (1918, fig. 30 A). In most similar specimens which have come to my notice the rudiments of adult leaves are present behind the growing point. It is probable that Campbell's figure has largely been responsible for the perpetuation of the belief that the thallus is normally cordate.

S. stipitatus stands apart from all other species credited to the genus by a number of features of the bottles in the female plants, namely, their stalk, their double-layered specialized wall, and the fact that their full development does not occur unless the archegonium is fertilized. All other species are essentially alike in their vegetative appearance; the main specific differences are based on the structure of the spores. In some instances critical work on the validity of the differences is desirable. It has been suggested that the Californian *S. cristatus* Howe is without close relatives (Howe, 1899; Allen, 1936). The early separation of the individual spores which it shows is known to occur also in some strains of *S. donnellii* (Siler, 1934). The fact that the foot remains attached to the sporophyte if one pulls the latter out depends on the persistence of the calyptra in this species, as mentioned above, as is a feature shared by others (e.g. *S. hians* Haynes, 1910). Allen (1936, p. 847) stated that the thallus lobes are also somewhat different from those of other species. This may be so in cultures; however, in the abundant local field material of *S. cristatus* I have found myself consistently unable to distinguish between it and *S. texanus* (or *S. michelii*? cf. Reimers, 1936), with which it usually is associated, without reference to the spores. The remaining unusual feature of *S. cristatus* is the less pronounced differentiation of the sex chromosomes.



Figs. 35–42. *S. stipitatus*. Chromosomes drawn from fresh acetocarmine squashes. Fig. 35. Male, prophase. Fig. 36. Male, pro-metaphase. Figs. 37, 38. Male, metaphase. Figs. 39–40. Female, prophase. Figs. 41–42. Female, metaphase. Figs. 35, 37 from young antheridia. Fig. 38 from more mature antheridium, the rest from growing points.

Campbell (1896*b*, *c*) described the genus *Geothallus* from material originating from San Diego, California, the only known locality to date. The elusive plant has been gathered there since by Prof. A. W. Haupt of the University of California at Los Angeles. According to Campbell, the plant is closely related to *Sphaerocarpos*. I have had the opportunity to examine the late Prof. Campbell's original slides, and Prof. Haupt kindly made available some preserved material. These specimens conform to the original excellent descriptions. The most striking feature of the material is the presence of a broad tuberous swelling on the lower side of the midrib. The lateral 'leaves' are very well developed.

Middle lobes are probably also present, but this should be confirmed on freely branching attenuate material. In addition, odd lobes sometimes occur among the bottles on the broad midrib. Similar odd lobes can be seen in occasional specimens of species of *Sphaerocarpos*, including *S. stipitatus*. Male and female plants of *Geothallus* are roughly of the same size. The only other recorded differences between *Geothallus* and *Sphaerocarpos* are found in minor details of the reproductive structures; in particular the stalk of the antheridia is somewhat more massive, and the sporophyte foot is more deeply embedded. I believed it not unlikely that the differences between the vegetative development of the plants of *Geothallus* and *Sphaerocarpos* are merely an expression of better nutritive conditions and the broadening of the midrib in the former, both features resulting from the presence of the tuber, and that the two genera should be united. However, recently I became acquainted with the living plant through the courtesy of Mr Gene Newcomb who collected specimens and soil-samples for me at San Diego. In culture I have obtained thalli very much like those of *Petalophyllum* which have sprouted typical *Geothallus* lobes.[1] It is clear that *Geothallus* needs further study.

The differences which separate *S. stipitatus* and *S. tuberosus*, respectively, from the other species of the genus include structural features. The residual species are very similar to each other, except for their spores. The genus as here understood can be divided in accordance with the following simple key, which lists the acceptable species to date:

Bottles of female plant sessile, with single-layered wall
    S. cristatus Howe, *S. donnellii* Austin, *S. drewei* Wigglesworth, *S. hians* Haynes, *S. michelii* Bellardi (type of genus),[2] *S. texanus* Austin, incl. var. *europaea* (Lorbeer) Müller[2]
Bottles of female plants stalked, with double layered wall
    S. stipitatus Bischoff ex Lindenberg

Of the species of *Sphaerocarpos* it is only *S. stipitatus* which is restricted to the Southern Hemisphere; the only other species which has been recorded from there (Chile, Argentina) is *S. ?texanus*. The Chile-South Africa disjunction shown by *S. stipitatus* is well known in the liverworts; *Marchantia berteroana* Lehm. & Lindenb. (syn. *M. tabularis* Nees) is the classical example. However, it can be said of the evanescent *Sphaerocarpos* that to gather it one first has to know it, and *S. stipitatus* may ultimately well be shown to have a general antarctic distribution. It was only recently that *Riella* was found in Australia (Banwell, 1951).[3] Africa appears to be the main centre of the genus *Riella*. Most of its species are found either in the north (Trabut, 1942) or south (Wigglesworth, 1937) of that continent. The currently recognized main centre of the genus *Sphaerocarpos*, on the other hand, is the Pacific coast of the United States, where four of the eight species occur, and three of them as endemics.

Following his discovery of the sex chromosomes, Prof. Allen realized the suitability of *Sphaerocarpos* for genetical investigations, and a vast body of work on the subject has since been done (cf. Allen, 1945). The genus has also yielded much basic information on the structure and function of sex chromosomes (Lorbeer, 1941). Most of these studies have been on *S. donnellii*. *S. stipitatus*, which has somewhat 'more morphology', might form an even more favourable subject.

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[1] Buch, Evans & Verdoorn (1938), in their check list, removed *Geothallus* from the neighbourhood of *Sphaerocarpos*, and placed it between *Fossombronia* and *Petalophyllum*, a treatment which does not appear to have been followed by anyone, and which was based on an earlier and equally unexplained arrangement by Verdoorn. Prof. Evans himself listed *Geothallus* again with *Sphaerocarpos* in the following year (1939).

[2] See Reimers (1936), and cf. Allen (1945, p. 269) and Thompson (1948), for discussion of taxonomic and distribution problems in these species.

[3] This plant, *R. halophila* Banwell, also possesses stalked bottles in the female.

The order Sphaerocarpales

Sphaerocarpos and its odd aquatic ally *Riella* have been difficult to place in an overall system of the bryophytes. Vegetatively they show jungermannioid features, the development of their sex organs is in keeping with the plan asserted characteristic for the Marchantiales, and their sporophytes are essentially like that of the marchantioid *Corsinia.* They therefore have been placed in either the Jungermanniales or the Marchantiales by different authors, and the latter treatment is still favoured by certain current workers. The gametophyte of *Sphaerocarpos* shows a striking resemblance to that of *Fossombronia,* which may be merely the result of converging evolution. The purported differences between the development of the sex organs, especially that of the antheridia, in the Marchantiales and Jungermanniales form a subject in need of critical review. The literature contains examples which throw doubt on their validity (e.g. Goebel, 1910, on *Monoselenium,* and cf. Campbell, 1896*c*, on *Geothallus tuberosus*). The structure of the sporophyte in itself is insufficient reason for exclusion of the plants from the Jungermanniales, if it is borne in mind that in the majority of other bryophytic groups reduction to the *Sphaerocarpos* level is encountered. Cavers (1910) solved the dilemma by proposing the order Sphaerocarpales, a proposal which has gained wide acceptance. *Naiadita,* the only fossil bryophyte so far recognized which tells us something new, may possibly be an ally of *Sphaerocarpos* and *Riella* (Harris, 1938, 1939). If this is correct, the evidence for regarding the Sphaerocarpales as an independent line is considerably strengthened.

Summary

Sphaerocarpos stipitatus Bisch. ex Lindenb. (syn. *S. berterii* Mont.) is re-described from the original material gathered in Chile in 1829. Material recently discovered in South Africa is shown to belong to the same species. Detailed studies of structure, development and cytology were made on the South African plants, both preserved and in culture.

The genus *Sphaerocarpos* is reviewed. It is re-emphasized that *Sphaerocarpos* normally has 'leafy' gametophytes, with a distinct and definite arrangement of the appendages. The general systematic position of the Sphaerocarpales is discussed.

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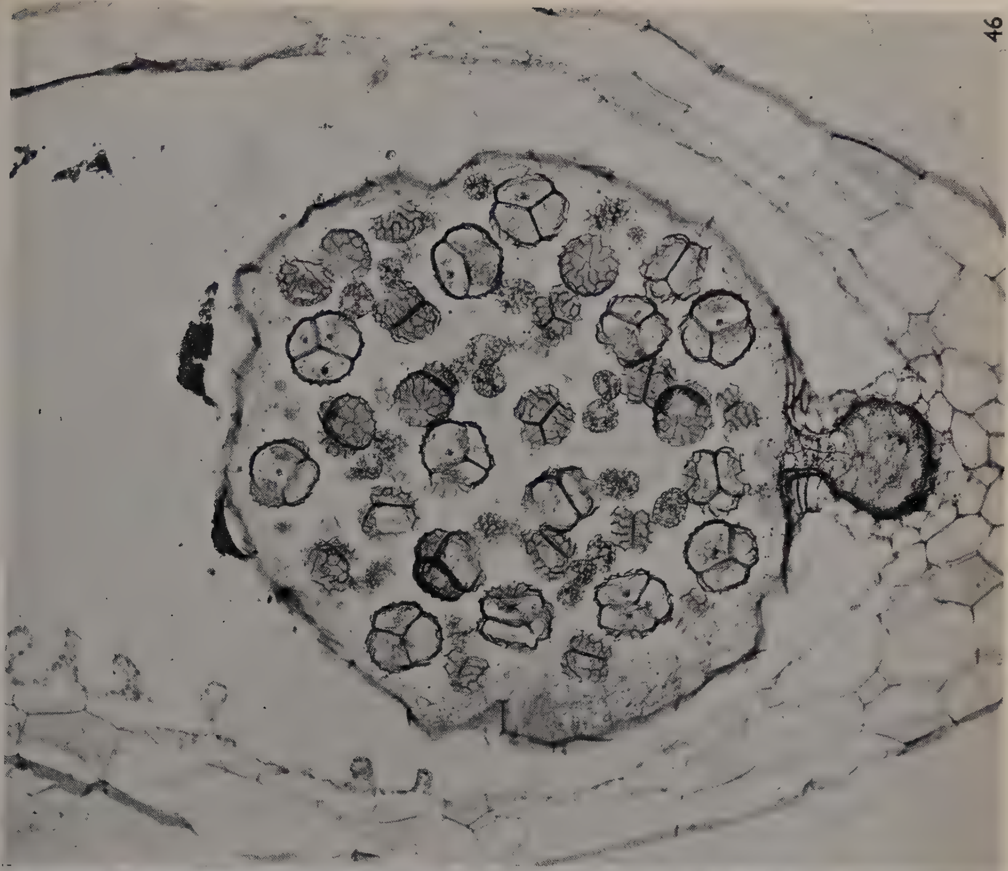

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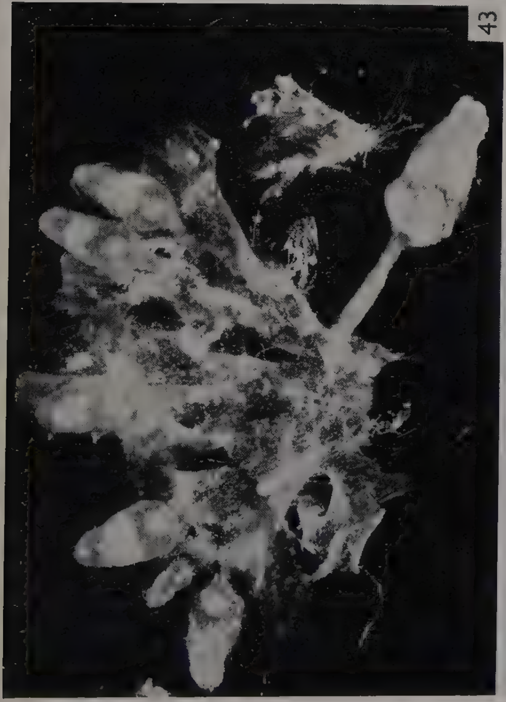

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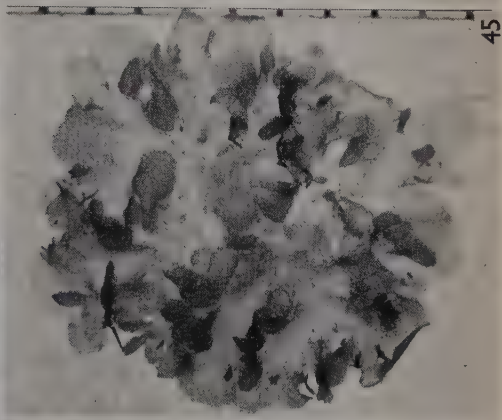

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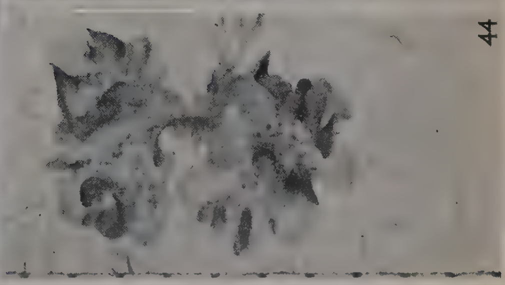

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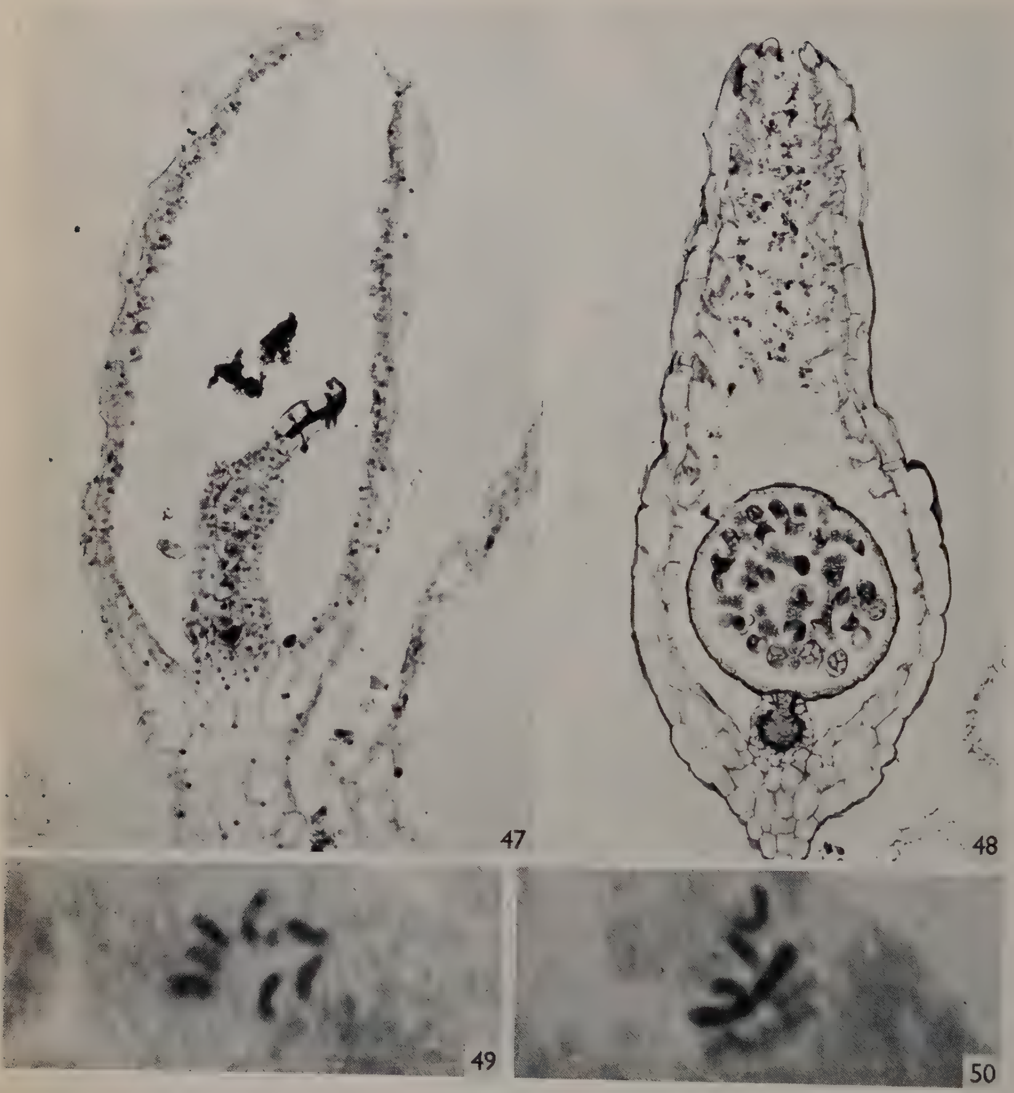
Sphaerocarpos stipitatus



Sphaerocarpos stipitatus

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EXPLANATION OF PLATES 14 AND 15.

(All photographs by Mr Victor Duran.)

Figs. 43–46. *Sphaerocarpos stipitatus*. Material from Chile. Fig. 43. Fragment of female plant, male plant. × 14. Material from South Africa. Fig. 44. Male plant. Fig. 45. Female plant, growing on agar. × 6. Fig. 46. Section through mature sporophyte, preserved in the field. × 104.

Figs. 47–50. *S. stipitatus*. South Africa. Material preserved in the field. Fig. 47. Young bottle, archegonium, and embryo. × 140. Fig. 48. Bottle with developing sporophyte in calyptra. Shortly after meiosis. Contents of capsule still contracted away from wall. × 53. From cultures. Figs. 49–50. Male and female chromosome sets. Metaphase. Same as Figs. 37, and 41, but after preparations made permanent. × 3000.

The anatomical structure of the Xanthorrhoeaceae Dumort.

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(With 98 Text-figures)

[Read 19 November 1953]

INTRODUCTION

Metcalfe & Chalk in their *Anatomy of Dicotyledons* (1950) attempted to summarize our present knowledge of the comparative anatomy of the vegetative organs of the numerous families of which the group is comprised. Although our knowledge of the dicotyledons is still far from complete, the monocotyledons have received much less attention from anatomists, and there are, indeed, certain families that have scarcely been investigated at all. One such family, which has received comparatively little attention is the Xanthorrhoeaceae, a group consisting of xeromorphic plants from Australia. The present paper deals with this family, and the work was undertaken in the hope that it would serve as a contribution to our knowledge of the systematic anatomy of the group. As the available material was limited, only one or two samples from the different organs of most of the species have been examined. Where it has been possible to examine a wider range of material of any one species, however, it has been found that those characters that are important for diagnostic purposes remain constant. For example, in *Acanthocarpus preissii* Lehm., although leaves that were 4·5 mm. broad as well as others 1·5 mm. wide were examined, both kinds of leaves differ only in the number of vascular bundles and the accompanying sclerenchyma bands, but no fundamental structural variations have been noted.

MATERIALS AND METHODS

It has been possible to examine nearly all the species belonging to the eight genera of the Xanthorrhoeaceae, but for some of them only leaf material was available. Wherever possible, however, attention has also been devoted to the other vegetative parts of the plants. Some of the specimens, preserved in formalin acetic alcohol, had been sent to the Jodrell Laboratory from Tasmania by Dr W. M. Curtis. A few living specimens from the Gardens at Kew were also available for investigation. The remaining material was taken from specimens in the museums and herbarium at Kew.

The dried specimens were boiled in water and subsequently stored in formalin acetic alcohol until required for use. Sections were cut with a sliding microtome, and it was not necessary for the material to be embedded in paraffin wax or any other medium. Stains used for the permanent slides were haematoxylin and safranin. Sections mounted in glycerine were stained with an alcoholic solution of Congo red and Chrysoidin (Réactif Génévois). In many cases Sudan IV has been used for staining the cuticle. For the examination of leaves sections of the middle part of the mature lamina have been used. When investigating the xylem elements the organs have been macerated. This was done in a mixture of equal parts of 5 % nitric acid and 5 % chromic acid in which the material was kept for 12–18 hr. at a temperature of about 60° C. After washing, the tissue was teased out carefully on slides (Cheadle, 1942). Sometimes this macerating fluid was not strong enough, and then the material examined was first boiled in a 10 % aqueous solution of potash, washed in water, kept for a few minutes in concentrated chromic acid and washed thoroughly (Boodle, 1916).

When examining the macerated material, attention was devoted especially to the elements of the metaxylem. Some of the drawings have been done by means of a microprojector and others with a camera lucida.

ANATOMICAL DESCRIPTIONS

(1) *Xanthorrhoea* Smith

Plants consisting of short rhizomes and a tree-like stem. Leaves long and linear, their bases remaining attached to the stem after the old leaves have fallen off. Nearly all the species of the genus have been examined.

Leaf

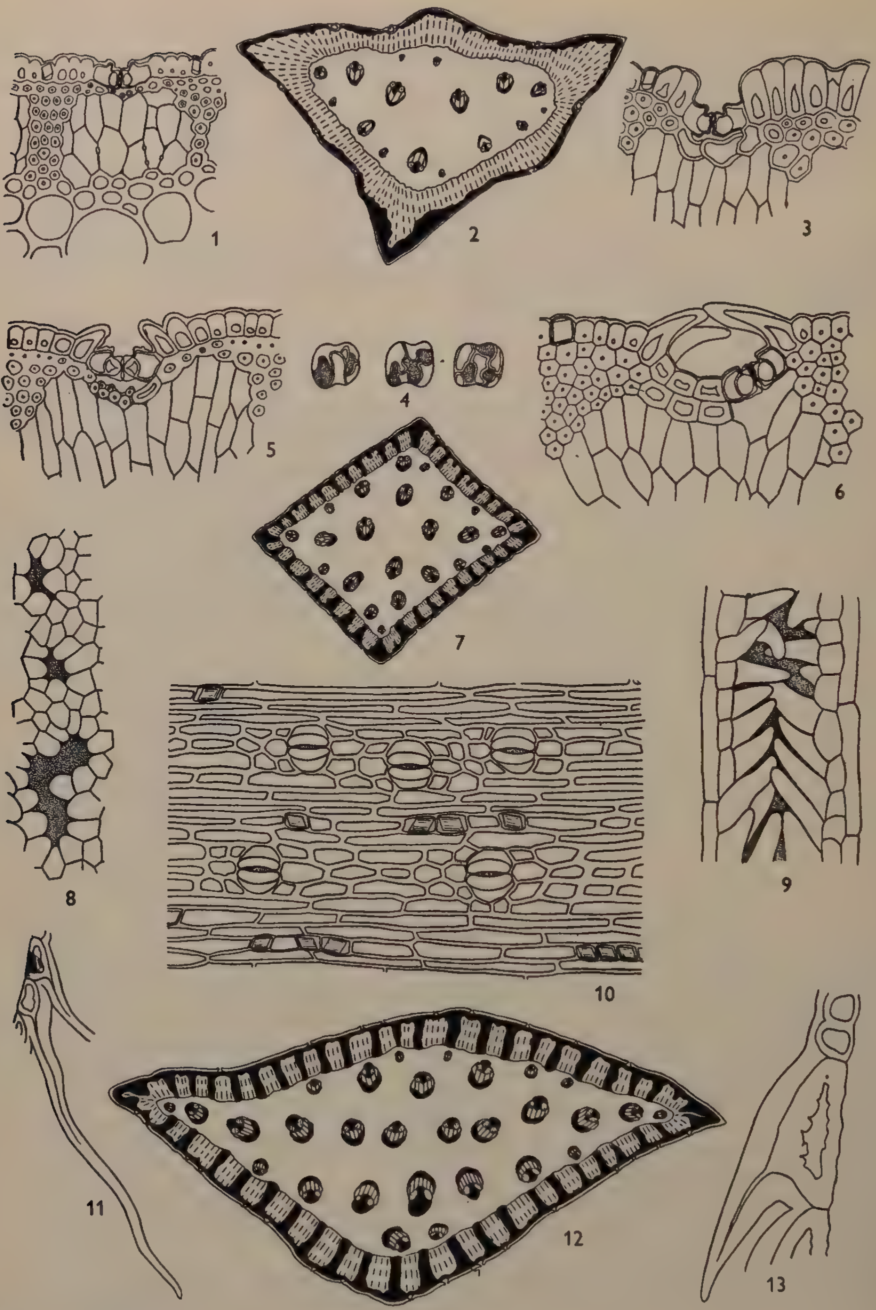
The leaves are isolateral and more or less triangular, spindle-shaped or quadrangular in cross-section. In transverse sections the leaves exhibit two zones. The outer of these consists of the epidermis, the palisade assimilating tissue and sclerenchyma; the inner zone being made up of a pith-like ground tissue with numerous vascular bundles embedded in it (Figs. 2, 7 and 12). The epidermis is mostly composed of cells with very much thickened walls and small lumina, but the subsidiary cells stand out in contrast to the remainder because of their much larger lumina. A relatively thick cuticle covers most of the epidermis, but a thinner layer is present over the stomatal cells (Figs. 1, 3, 5 and 6). The stomata are arranged in strips of the epidermis that lie parallel with the axis of the leaf. These strips, which overlie the assimilating tissue, alternate with strips of epidermis lying above the mechanical tissue (sclerenchyma). The cells of the portions of the epidermis that lie above the assimilating tissue are comparatively short in surface view, and contrast with the portions of the epidermis above the sclerenchyma where the cells are longer and stomata are absent. The epidermis above the sclerenchyma also includes small thin-walled, almost cubical cells containing rhomboidal crystals (Figs. 1, 3, 6 and 10). Four types of stomata, which can be recognized by their positions in relation to the leaf surface, have been observed in different species of *Xanthorrhoea*: (1) Stomata at the same level as the neighbouring epidermal cells (*X. arborea*, *X. bracteata*, *X. semiplana*, *X. tateana* and *X. quadrangulata*) (Figs. 1 and 10). (2) Stomata somewhat sunken and surrounded by epidermal cells without papillae (*X. minor*, *X. australis*, *X. hastile* and *X. brevistyla*) (Fig. 3). (3) Stomata sunken, but accompanied by epidermal cells with papillae which are inclined towards the stomata (*Xanthorrhoea* sp. aff. *X. reflexa*, *X. preissii*) (Figs. 5 and 8). (4) Stomata in furrows which arise in the epidermal strips; the furrows being overarched from both sides by papillae which extend from the epidermal cells (*X. gracilis* and *X. macronema*) (Figs. 6 and 9). Each stoma could be seen to be surrounded by four subsidiary cells in all of the species examined except those in which the papillae obscure them (Fig. 10).

Short, very thick-walled, bent hairs are confined to the leaf margins (Fig. 13); much longer hairs occur at the leaf margins in *X. hastile* and at the margins and on the abaxial surface of the leaf-sheath of *X. gracilis* (Fig. 11).

Hypodermis consisting of sclereids. Projections from the surrounding sclereids extend into the substomatal chambers, in *X. hastile*, *X. bracteata*, *X. arborea*, *X. australis*, *X. quadrangulata* and some specimens of *X. minor* collected by Sharman, 1951 and by Rodway, 1951 (Figs. 1, 3 and 4).

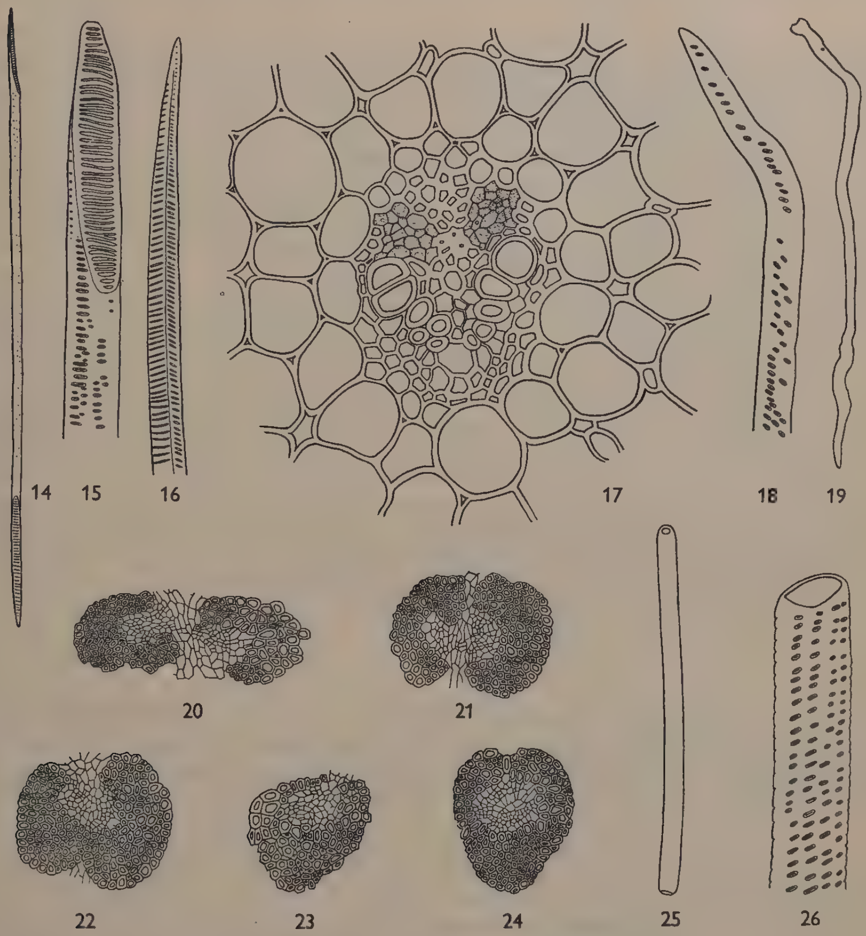
In *X. brevistyla*, *X. preissii*, *Xanthorrhoea* sp. aff. *X. reflexa* and in some specimens of *X. minor* (Morrison, 3021 and 1487, Kew Herb.) there are twisted, sponge-like sclerosed cells, similar to those that are known to occur in *Kingia* (Tschirch, 1881) (Fig. 54) and which line the interior of the substomatal chambers. No such structures occur in *X. gracilis* and *X. macronema*.

Palisade tissue consisting of two to four layers of cells. Small elliptical intercellular



Figs. 1–13. *Xanthorrhoea.* 1. *X. arborea*, T.S. leaf, stomatal region, × 210. 2. *X. macronema*, T.S. leaf, × 17. 3. *X. minor*, T.S. leaf, stomatal region, × 210. 4. *X. arborea*, papillose projections of the sclereids surrounding the substomatal chambers, seen from surface view by focusing on the subepidermal layers, × 210. 5. *Xanthorrhoea* sp. aff. *X. reflexa*, T.S. leaf, stomatal region, × 210. 6. *X. gracilis*, T.S. leaf, stomatal region, × 210. 7. *X. quadrangulata*, T.S. leaf, × 17. 8. *Xanthorrhoea* sp. aff. *X. reflexa*, epidermis above the photosynthetic tissue, surface view, × 210. 9. *X. gracilis*, epidermis above the photosynthetic tissue, surface view, × 210. 10. *X. arborea*, epidermis in surface view, × 210. 11. *X. gracilis*, L.S. hairs at the margins of the leaf base, × 210. 12. *Xanthorrhoea* sp. aff. *X. preissii*, T.S. leaf, × 17. 13. *X. minor*, L.S. stiff hairs at the margins of the lamina, × 210. *Explanation of the conventions used in all the diagrams:* solid black = sclerenchyma; vertical parallel lines = xylem; broken lines = photosynthetic tissue; dotted areas = phloem; uncoloured = parenchymatous tissues.

spaces very often occur between the inner palisade cells (Fig. 1). Elongated, somewhat thick-walled cells, which lie parallel to the long axis of the leaf, occur amongst the palisade cells. These cells are similar to the raphide cells of *Calectasia* and *Lomandra.* The palisade tissue is interrupted by bands of sclerenchyma in all the species except in *Xanthorrhoea macronema*, where the assimilating tissue is continuous and the sclerenchyma surrounds it (Fig. 2). Where sclerenchyma bands exist they merge tangentially at the leaf base and produce a continuous sheath (as seen in *X. australis* and *X. arborea*). On the inner side of the sclerenchyma and palisade tissue there is a thick-walled pith-like parenchymatous tissue with conspicuous intercellular spaces (Fig. 17). Cells, each of which is filled with a brown mass, probably resin, occur in the mesophyll. Each vascular bundle includes two phloem groups, and, in cross-section, shows a V-shaped xylem (Fig. 17). The metaxylem in *X. minor* and *X. australis* partly consists of elements which are probably vessels with very oblique scalariform perforation plates (Figs. 14, 15).



Figs. 14–26. *Xanthorrhoea minor*. 14. Vessel member from a leaf, × 50. 15. Part of a vessel member from a leaf, × 210. 16. Part of a tracheid from a leaf, × 210. 17. T.S. vascular bundle from a leaf with V-shaped xylem and two strands of phloem, × 210. 18. Part of a tracheid from a stem, × 210. 19. Stem tracheid, × 50. 20–24. T.S. vascular bundles with U-shaped xylem, showing various stages in their approaching and fusing to form an amphivasal bundle, × 50. 25. Vessel element from a root, × 50. 26. Part of a vessel element from a root, × 210.

Elements which could definitely be recognized as tracheids were also seen (Fig. 16). Elements with annular and spiral thickening, believed to be derived from the protoxylem, have also been noted.

Stem

Outer portion of the bark consisting of a black to brown mass of broken and partially decomposed cells and resin. Below this there is a zone of parenchymatous cells containing brown granular bodies, and groups of sclereids between them. The next zone towards the centre consists of a translucent parenchyma. According to Osborn (1916) many cells in this region contain raphides. Between this zone and the innermost parenchyma in which the vascular bundles are embedded, there is a wide cambial zone. This cambium is mentioned by Arber (1925) as producing secondary vessels, and by Osborn (1916) as producing parenchyma cells towards the bark within the outermost cells of which resin is secreted. This gives rise to the resin sheath of the bark.

The vascular bundles of the stem either exhibit U-shaped xylem or they are amphivasal. Various stages have been seen (Figs. 20–24) in which two bundles with U-shaped xylem strands gradually approach one another and fuse to form an amphivasal bundle. This confirms Jeffrey's opinion that the amphivasal bundle is derived from foliar bundles that become crowded together and fuse at the nodes (Jeffrey, 1917). Although this is true of *Xanthorrhoea* it is also possible that Arber's opinion, that amphivasal bundles may have arisen by the arms of the V-xylem embracing the phloem (Arber, 1925), is applicable to some of the other genera of the Xanthorrhoeaceae.

Cells containing rhomboidal crystals occur around the bundles. Xylem consisting of sinuous tracheids (Figs. 18, 19) in *X. minor*. The length of the tracheids varied from 1 to 3 mm. and their maximum diameter was about 30μ.

Root

Inner part of the cortex sclerenchymatous. Endodermis consisting of cells with typical U-shaped thickenings. The tracheal elements in the xylem of *X. minor* are vessels with simple perforations (Figs. 25, 26) as seen. Their lengths have been found to vary from 0·960 to 1·280 mm. and their diameters from 37 to 56μ.

Material examined

X. arborea R.Br., Kew Museum specimen.
X. australis R.Br., N.E. Tasmania. G. Sharman (1951). Received through Dr W. M. Curtis.
X. bracteata R.Br., Woolls, Kew Herb.
X. brevistyla Herbert, D. A. Herbert, Kew Herb.
X. gracilis Endl., Morrison, 8284, Kew Herb.
X. hastilis R.Br., Rodway, 1768, Kew Herb.
X. macronema F. Muell., McGilivray, Kew Herb.
X. minor R.Br., (*a*) N.E. Tasmania, 1. G. Sharman (1951), 2. E. P. Rodway (1951); received through Dr W. M. Curtis. (*b*) Morrison, 3021 and 1487, Kew Herb.
X. preissii Endl., Pritzel, 1005, Kew Herb.
X. sp. aff. *X. preissii* Endl., Morrison, 12202, Kew Herb.
X. quadrangulata F. Muell., Kew Museum specimen.
X. sp. aff. *X. reflexa* Herbert, Morrison, 8286, Kew Herb.
X. semiplana F. Muell., Hort. Kew (1952).
X. tateana F. Muell., Hort. Kew (1952).

(2) *Lomandra* Labill.

Plants consisting of rhizomes bearing simple or branched aerial stems. Stems short, the longest not exceeding 45 cm. Leaves stiff. Those at the base are long (sometimes up to 60 cm.), linear and aggregated. Smaller leaves are scattered on the branches. Scapes terminal. Thirty-three species have been examined out of the total of about thirty-five that have been described.

Leaf

The leaves are flattened terete or half-cylindrical. Epidermis, in most species, composed of cells with walls which are only moderately thickened, but in some species (for example, *L. caespitosa*, *L. filiformis*, *L. juncea*, *L. drummondii*, *L. dura*, *L. sororia*, *L. pauciflora*, *L. caespitosa* ± *L. micrantha* and *L. confertifolia*) the epidermal cells above the sclerenchymatous bands, that occur beneath one or both leaf surfaces, are fibre-like. Cuticle moderately to very thick (Figs. 27–30, 32, 34, 35 and 37). The epidermal cells above the bands of sclerenchyma, in which the vascular bundles are embedded, are conspicuously longer than the others. The stomata, each of which is surrounded by four subsidiary cells, occur on both surfaces of the leaf, but are confined to the portion of the epidermis overlying the strips of tissue between the sclerenchymatous bands. The strips of tissue, between the sclerenchyma, are situated, in most of the species, in furrows of various depths. On the other hand, in some species such as *L. multiflora*, *L. caespitosa*, *L. hermaph. andrewsii*, *L. spartea*, *L. sonderi*, *L. glauca* and *L. micrantha*, the portion of the epidermis above the photosynthetic tissue is at the same, or almost at the same, level as the remainder.

Large polyhedral or rhomboidal crystals occur in most species where they are situated in specialized epidermal cells (Fig. 30) or in similar cells just below the epidermis (Figs. 28 and 32) overlying the sclerenchymatous bands. In *L. caespitosa* and *L. turbinata* the epidermal or hypodermal crystals are arranged in two parallel rows. In *L. caespitosa* small rod-like crystals were sometimes observed in addition to the polyhedral types that have just been mentioned. Specially large cells (idioblasts) are also to be seen in the mesophyll, where each of them contains one or more elongated crystals which sometimes resemble, and frequently are, raphides. Both of these types of crystalliferous cells occur in many species. In *L. rigida*, *L. hermaph. andrewsii*, *L. suaveolens* and *L. purpurea* rhomboidal or polyhedral crystals have been seen in cells connected with the vascular bundles and their sclerenchyma.

Scale-like hairs each consisting of a row of papilla-like epidermal cells with very thick walls occur in some species above the sclerenchyma. Their orientation is transverse to that of the leaf axis (Figs. 35 and 38). These hairs occur at the margins of the leaf and on the abaxial surface in *L. filiformis*, *L. banksii* and *L. sororia*, but are somewhat less developed in *L. dura*, and are present only at the margins in *L. rupestris*, *L. collina* and *L. drummondii*. Similar hairs, but consisting of much shorter papillae, occur on the leaf margins of *L. endlicheri* and *L. longifolia*. Prominent unicellular papillae occur above the sclerenchyma bands at the margins and on the abaxial surfaces of the leaves of *L. preissii* (Fig. 34) and above the photosynthetic tissue on one or both leaf surfaces in *L. hastilis*, *L. leucocephala*, *L. juncea*, *L. micrantha*, *L. multiflora*, *L. banksii*, *L. dura*, *L. sororia* and *L. effusa*. In some species the papillae overarch the furrows in which the photosynthetic tissue is situated from both sides, and in this respect resemble those in *Xanthorrhoea gracilis* and *X. macronema*. Very small papillae occur at the leaf margins of *Lomandra benthamiana* and above the photosynthetic tissue in *L. andrewsii*, *L. turbinata*, *L. rupestris*, *L. collina*, *L. sonderi*, *L. sericea* and *L. pauciflora*. The photosynthetic tissue occurs below the epidermis of both surfaces of the leaf. In some species it consists of isodiametric cells (Fig. 37) and in others of more or less typical palisade cells (Figs. 28, 36). In almost all species the photosynthetic cells have broad papillose projections, which resemble those of *Kingia* and *Calectasia*. Very small rounded intercellular spaces are formed between these projections (Fig. 36). The central part of the mesophyll is pith-like (Figs. 33, 39, 40, 43 and 44) in *L. rigida*, *L. longifolia*, *L. spartea*, *L. juncea*, *L. turbinata* and *L. dura*, but more or less constitutes a continuation of the photosynthetic tissue (Figs. 41, 42) in the remaining species. In many species, very small intercellular spaces, resembling those that occur between the palisade cells, are formed between the cells of the central mesophyll. The assimilating tissue is interrupted by the fascicular sclerenchymatous I-girders. These girders extend to the epidermis of the leaf in all species except *L. pauciflora*. The photosynthetic tissue, especially on the abaxial surface of the leaf, is also interrupted by bands of sclerenchyma occurring between the bundles (Figs. 33, 39 and 41–44). An additional tissue occurs in *L. longifolia* and *L. confertifolia* where it occurs opposite the interfascicular sclerenchyma bands, interrupting the adaxial photosynthetic tissue. This is a tissue of thin-walled cells without chloroplasts (Fig. 37), which occurs in regions where there are narrow and shallow longitudinal furrows on the adaxial surface of the leaf. In the central part of the mesophyll very small groups of small sclereids occur sometimes. Sheaths, each of which consists of one layer of large, somewhat thick-walled cells without chloroplasts, accompany the vascular bundles (Figs. 33, 39 and 41–44). The metaxylem includes long and pitted tracheids. Elements with spiral and annular thickening, believed to be derived from the protoxylem, have also been noted.

Stem

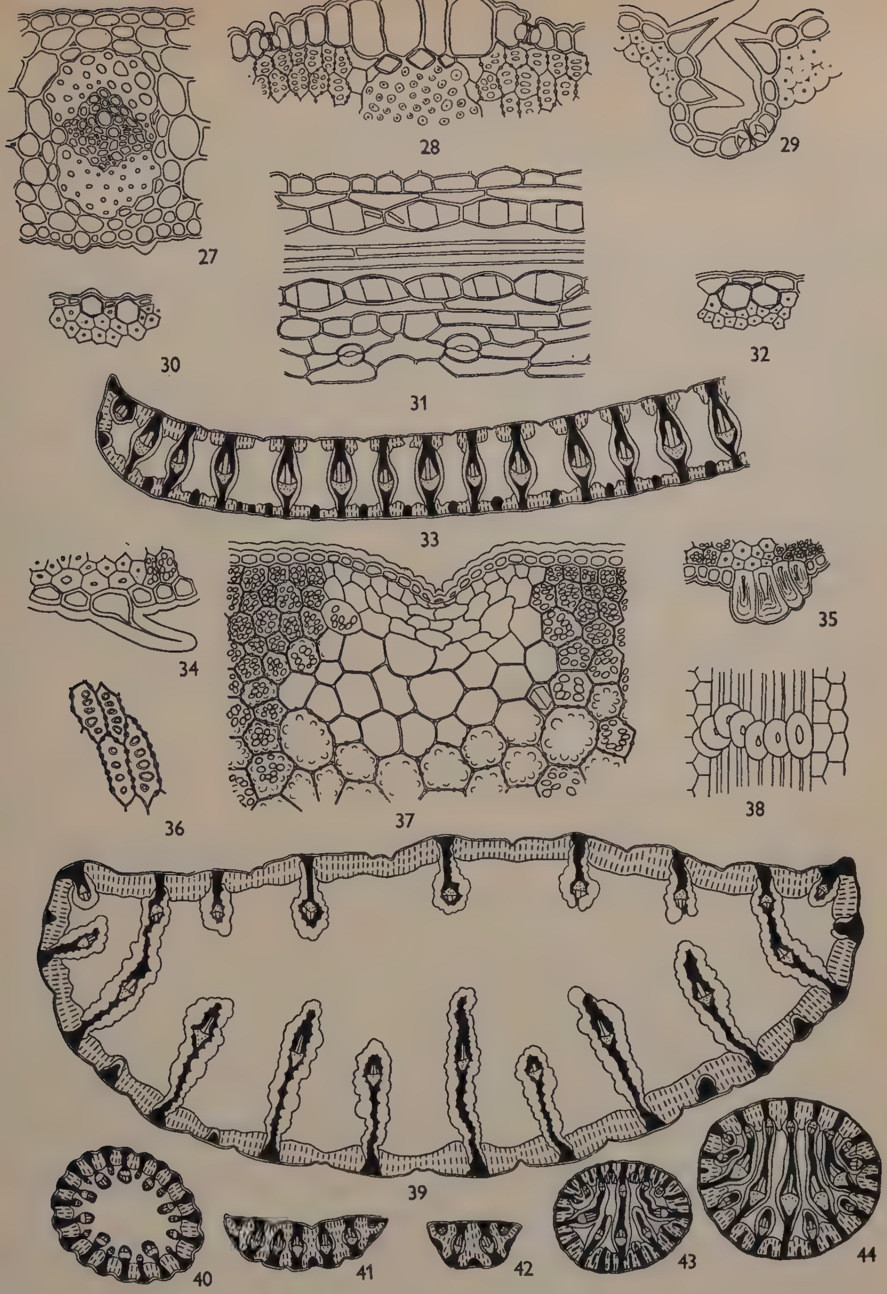
The epidermis consists of cells with very thick walls and covered by a very thick cuticle. An incomplete, single layer (and in some places two layers), of sclerenchyma sometimes occurs below the epidermis. The cortical parenchyma is present immediately within the sclerenchyma. This tissue is homogeneous in *L. pauciflora* but consists of two distinct zones in *L. filiformis* and *L. confertifolia*. The outer zone consists of cells of which the walls are somewhat lignified or suberized. Some of these cells contain thin, elongated raphide-like crystals as noted in *L. confertifolia*. The inner cortical zone consists of cells of which the walls are thinner and not lignified or suberized. In the central cylinder the numerous amphivasal bundles are embedded in a very thick-walled parenchyma. The xylem consists of somewhat sinuous tracheids. A cambial zone has also been seen in the stems of *L. flexifolia* and *L. glauca*, where it occurs immediately beneath the thin-walled zone of the cortical parenchyma. This cambium produces the secondary tissue which can easily be recognized. Bundles of raphides occur in most of the cells produced by the cambium towards the outside. The cells of the crystalliferous zone are similar in shape to the cambial cells that are still active. A periderm has been noted below the epidermis in *L. glauca*. The length of the tracheids in *L. confertifolia* varies from 2·00 to 2·72 mm. and their width from 16 to 19μ.

Rhizome

Below the epidermis there are several layers of cells with somewhat thickened suberized walls. Passing towards the centre, the next tissue is the cortical parenchyma which includes some large elliptical cells containing raphides. A pseudo-cambium occurs between the cortex and the more central parenchymatous tissue, in which the vascular bundles are embedded. This meristematic zone which has been seen in *L. preissii*, *L. filiformis* and *Lomandra* sp. aff. *L. endlicheri* (Fig. 46), gives rise on the inside to additional ground parenchyma and vascular bundles. The vascular bundles themselves are amphivasal, and the tracheal elements of the xylem consist of sinuous tracheids (Fig. 45), those of *L. preissii* having an average length of 0·8 mm. and a maximum diameter of 22μ.

Root (Fig. 47)

The inner part of the cortex is sclerosed. The endodermis is made up of cells with typical U-shaped thickenings, and, within the endodermis, there is a single layer of pericyclic cells with wide lumina. The tracheal elements in the xylem are vessels with simple



Figs. 27–44. *Lomandra.* 27. *L. pauciflora*, T.S. leaf in the region of a vascular bundle, × 210. 28. *L. hermaphrodita*, T.S. leaf showing the large epidermal cells above the sclerenchymatous bands, and the hypodermal crystals, × 210. 29. *L. leucocephala*, T.S. leaf, in the stomatal region, × 210. 30. *L. filiformis*, T.S. leaf, showing crystals in the epidermal cells above the sclerenchymatous bands, × 210. 31. *L. caespitosa*, leaf epidermis in surface view showing crystals arranged in two parallel rows of cells above the ends of the sclerenchymatous bands, × 210. 32. *L. endlicheri*, T.S. leaf, showing crystals in hypodermal cells above the sclerenchymatous bands, × 210. 33. *L. longifolia*, T.S. leaf, × 17. 34. *L. preissii*, T.S. leaf showing a large papilla above a sclerenchymatous band on the abaxial leaf surface, × 210. 35. *L. filiformis*, T.S. leaf, showing a multicellular scale-like hair on the abaxial leaf surface above the sclerenchyma, × 210. 36. *L. hastilis*, palisade cells with papillose projections and intercellular spaces which appear rounded in transverse section, × 210. 37. *L. longifolia*, T.S. leaf showing special thin-walled, colourless cells interrupting the photosynthetic tissue in the furrow regions, × 210. 38. *L. filiformis*, multicellular, scale-like hair in surface view, × 210. 39. *L. rigida*, T.S. leaf, × 17. 40. *L. turbinata*, T.S. leaf, × 17. 41. *L. endlicheri*, T.S. leaf, × 17. 42. *L. endlicheri* (late dwarf form, ♂), T.S. leaf, × 17. 43. *L. spartea* T.S. leaf, × 17. 44. *L. spartea* (?) T.S. leaf, × 17

perforation (Fig. 48). The roots have been examined in *L. preissii*, *L. filiformis*, *L. endlicheri*, *L. collina* and *L. confertifolia*. The vessel elements of *L. preissii* vary in length from 1·04 to 1·70 mm. and they are usually about 32μ in diameter.

Key to the identification of Lomandra spp.

The following key has been drawn up to enable the different species of *Lomandra* to be identified from the anatomical characters of the leaves. The key is based exclusively on leaf characters for three reasons: (i) because the leaf is the organ of the plant that can most easily be collected; (ii) differences between species are more definitely portrayed in the leaf than in any other part of the plant; (iii) if the middle part of the mature lamina is always selected as standard material when making comparisons, it is easier to eliminate ontogenetic structural differences than it would be in stems or roots.

As only a limited amount of material was available for examination, attention has been directed especially to those diagnostic characters that are unquestionably constant and therefore reliable. It has not been found possible to separate every species on account of this limitation, and it will be seen in the key that some of them have consequently fallen into small groups.

It should be noted that it is necessary to examine strips of the epidermis in surface view, in order to determine whether crystals are present in the epidermis or subepidermis, and, when present, in which parts of the leaf they are to be found.

Key

1. (*a*) I-girders of fascicular sclerenchyma very rarely extending to the epidermis (Fig. 27). *L. pauciflora*
(*b*) All I-girders of fascicular sclerenchyma extending to the epidermis (Figs. 33 and 39–44). **2**

2. (*a*) At least one I-girder of fascicular sclerenchyma extends from the abaxial to the adaxial epidermis. **3**
(*b*) All I-girders of fascicular sclerenchyma surrounding the leaf extend to the epidermis at one end only (Fig. 40). *L. turbinata*

3. (*a*) At least one of the fascicular sclerenchymatous I-girders which extends to both leaf surfaces includes three or four separate vascular bundles. *L. juncea*
(*b*) Each fascicular sclerenchymatous I-girder including one or two vascular bundles. **4**

4. (*a*) Two vascular bundles present in one or more of the fascicular sclerenchymatous I-girders (Figs. 39, 43 and 44). **5**
(*b*) Each band of fascicular sclerenchymatous I-girder including one vascular bundle (Figs. 33, 41 and 42). **6**

5. (*a*) Crystals present in sunken cells just below the epidermis of both surfaces of the leaf. *L. rigida*
(*b*) Crystals absent from the epidermis and subjacent cells. *L. spartea*

6. (*a*) Crystals absent from epidermis and hypodermis. **7**
(*b*) Crystals present in the epidermis or hypodermis of one or both surfaces, or confined to the same layers at the leaf margins (Figs. 28, 30 and 32). **13**

7. (*a*) More or less prominent papillae present in the furrows in one or both surfaces of the leaf. **8**
(*b*) Papillae absent from the furrows. **11**

8. (*a*) Interfascicular bands of sclerenchyma present between the fascicular I-girders at one or both leaf surfaces (Figs. 33, 39 and 41–44). **9**
(*b*) Interfascicular bands of sclerenchyma absent. *L. leucocephala*

9. (*a*) Interfascicular bands of sclerenchyma confined to one leaf surface. *L. dura*
(*b*) Interfascicular sclerenchyma bands present below both leaf surfaces. **10**

10. (*a*) Low scale-like hairs, each consisting of a row of papilla-like epidermal cells, present on the abaxial surface of the leaf, when they occur above the sclerenchyma bands and are orientated transversely to the leaf axis (Figs. 35, 38). *L. banksii*
(*b*) Scale-like hairs absent. *L. hastilis*

11. (*a*) Interfascicular bands of sclerenchyma, situated between the fascicular I-girders, present below the epidermis on both leaf surfaces. **12**
(*b*) Interfascicular bands of sclerenchyma present below the epidermis on one leaf surface only. *L. longifolia, L. confertifolia*

12. (*a*) Interfascicular bands of sclerenchyma appearing radially elongated in transverse sections. *L. sonderi, L. sericea*
(*b*) Interfascicular bands of sclerenchyma appearing tangentially elongated in transverse sections. *L. montana*

13. (*a*) Crystals in the epidermal or hypodermal cells confined to the leaf margins. **14**
(*b*) Crystals present in the epidermal or hypodermal cells overlying all the sclerenchyma bands immediately below one or both leaf surfaces. **16**

14. (*a*) Crystals in epidermal or hypodermal cells present on both surfaces of the leaf at margins. **15**
(*b*) Epidermal crystals confined to the upper surface of the leaf margins. *L. sororia*

15. (*a*) Large papillae present above the sclerenchyma bands at the margins and on the abaxial surface of the leaf. *L. preissii*
(*b*) Papillae absent from the leaf surface. *L. drummondii*

16. (*a*) Crystals present in special cells immediately below the epidermis. **17**
(*b*) Crystals confined to the epidermis itself. **21**

17. (*a*) Hypodermal crystals above the sclerenchyma bands confined to the adaxial side of the leaf. *L. collina*
(*b*) Hypodermal crystals above the sclerenchyma bands present on both sides of the leaf. **18**

18. (*a*) More or less prominent papillae absent from the surface and margins of the leaf. *L. suaveolens*
(*b*) More or less prominent papillae present on both surfaces, and/or at the margins, of the leaf. **19**

19. (*a*) Small papillae confined to the leaf margins. *L. endlicheri*
(*b*) Small papillae present above the strips of photosynthetic tissue. **20**

20. (*a*) Epidermal cells above the sclerenchyma bands conspicuously tall (Fig. 28). *L. hermaphrodita*
(*b*) Epidermal cells above the sclerenchyma bands more or less the same height as, or even lower than, those between the sclerenchyma bands. *L. rupestris*

21. (*a*) Epidermal crystals present above all the sclerenchyma bands on the adaxial surface, and sometimes on the abaxial surface of the leaf margins as well. **22**
(*b*) Epidermal crystals present above all the sclerenchyma bands on both leaf surfaces. **23**

22. (*a*) Epidermal crystals confined to the adaxial surface. *L. effusa*
(*b*) Epidermal crystals present above all the sclerenchyma bands on the adaxial surface, as well as on the abaxial surface of the leaf margins. *L. filiformis*

23. (*a*) More or less prominent papillae present in the furrows above the photosynthetic tissue. *L. micrantha*
(*b*) Prominent papillae absent from the epidermis above the photosynthetic tissue. **24**

24. (*a*) Scale-like hairs, each consisting of a row of papilla-like epidermal cells with very thick walls, present at the leaf margins, where they are orientated transversely to the leaf axis. *L. glauca*
(*b*) Scale-like hairs absent. *L. caespitosa, L. odora, L. elongata, L. flexifolia*

Material examined

L. banksii (R.Br.) Ewart, Cunningham, 23, Kew Herb.
L. caespitosa (Benth.) Ewart, L. V. Lester Garland, Kew Herb. Andrews, 1036, Kew Herb.
L. collina (R.Br.) Ewart, Drummond, 116, Kew Herb.
**L. confertifolia* (F. M. Bail.) Fahn, Hubbard, 4164, Kew Herb.
L. drummondii (F. Muell.) Ewart, Drummond, 209, Kew Herb.
L. dura (F. Muell.) Ewart, Mueller, 1876, Kew Herb.
L. effusa (Lindl.) Ewart, Clowes, Kew Herb.
L. elongata (Benth.) Ewart, Mueller, Montana, Kew Herb.
L. endlicheri (F. Muell.) Ewart, Morrison, 10238, Kew Herb.
L. sp. aff. *L. endlicheri* (late dwarf form), Morrison, 16178 and 10240, Kew Herb.
L. filiformis (R.Br.) Britten, Morrison, 1486, Kew Herb.
L. flexifolia (R.Br.) Ewart, Clowes, Kew Herb.
L. glauca (R.Br.) Ewart, Bynoe, Kew Herb.
L. hastilis (R.Br.) Ewart, Maxwell, Kew Herb.
L. hermaphrodita (C. Andrews) C. A. Gardner, Andrews, 1034, Kew Herb.
L. juncea (F. Muell.) Ewart, Wilhelmi, Kew Herb.
L. leucocephala (R.Br.) Ewart, Chippendale & Constable, 17384, Kew Herb.
L. longifolia Labill., Morrison, 5042, Kew Herb.
L. micrantha (Endl.) Ewart, Drummond, 809, Kew Herb.
L. montana (R.Br.) L. Fraser & Vickery, Hooker, Mt. Tomah, Kew Herb.
L. multiflora (R.Br.) Britten, Rodway, October 1925.
L. odora (Endl.) Ewart, Drummond, Kew Herb.
L. pauciflora (R.Br.) Ewart, L. V. Lester Garland, Kew Herb.
L. preissii (Endl.) Ewart, Morrison, 12217, Kew Herb.
L. sp. aff. *L. preissii*, Morrison, 17067, Kew Herb.
L. purpurea (Endl.) Ewart, A. Dorrien Smith, 1910, Kew Herb.
L. rigida Labill., Mueller, 1876, Kew Herb.
L. rupestris (Endl.) Ewart, Drummond, 334, Kew Herb.
L. sericea (Endl.) Ewart, Koch, 2070, Kew Herb.
L. sonderi (F. Muell.) Ewart, Drummond, 59, Kew Herb.
L. sororia (F. Muell.) Ewart, Mueller, Capaspe, Kew Herb.
L. spartea (Endl.) Ewart, Preiss, 1533, Kew Herb.
L. suaveolens (Endl.) Ewart, Morrison, 1900, Kew Herb.
L. turbinata (Endl.) Ewart, Drummond, Kew Herb.

(3) *Kingia* R.Br.

The single species of this genus exhibits an erect, tree-like stem 2–9 m. high, bearing stiff linear leaves, 30–45 cm. long.

Leaf (Fig. 57)

Leaf isolateral; spindle-shaped in cross-section and exhibiting two distinct zones. Outer zones cortex-like and consisting of the epidermis and palisade tissue which is interrupted, and partly surrounded, by sclerenchyma. Inner zone consisting of a pith-like ground-tissue in which a row of vascular bundles is embedded. The bundles themselves are embedded in girders (bands) of sclerenchyma which are I-shaped in transverse

* **Lomandra confertifolia** (F. M. Bail.) Fahn, comb.nov.
Based on *Xerotes confertifolia* F. M. Bail, in Queens Agric. Journ. **25**, 11 (1910).

section, and their distal ends extend almost to the cortex-like zone that has just been described (Fig. 57). Epidermis consisting of almost cubical cells with somewhat thickened walls. Cuticle thick and extending between the epidermal cells to half the length of the anticlinal walls. The stomata, each of which is surrounded by seven or eight subsidiary cells (Fig. 55), are almost at the same level as the remainder of the epidermis and likewise covered by cuticle. Druses (cluster crystals) occur in most of the epidermal cells. Short, stiff, sloping multicellular hairs with very thick cell-walls present at the leaf margins (Fig. 58). Leaf bases bearded with long multicellular hairs, each of which consists of long, pointed, thick-walled cells (Fig. 56). Hypodermis consisting of sclereids. Twisted, sponge-like cells, termed 'Schutzzellen' by A. Tschirch (1881), with thick walls and covered by many projections, occur below the stomata, where they are believed to prevent excessive evaporation (Fig. 54). In the cortex-like zone below the sclereidal hypodermis there is a net of a sclerenchymatous tissue consisting of radially elongated cells. In cross-section this tissue appears as radial strips between the patches of palisade tissue (Fig. 57). Palisade tissue, as already described by Tschirch (1881), consisting partly of cells with papillose projections arranged in rows and partly of cells with annular contractions. Short papillae are also to be seen in the cells with the annular contractions. Elliptical or rounded intercellular spaces always occur between the 'annular' cells. With the cells which have papillose projections but no 'annular' contractions, on the other hand, the papillae of adjacent cells are dove-tailed between each other. If the papillae do not interlock in the manner just described, intercellular spaces are formed (Fig. 76). Very long and pitted tracheids occur in the metaxylem, and elements with annular and spiral thickening, believed to be derived from the protoxylem, have also been noted.

Stem

The stem probably increases in diameter by secondary thickening from meristem that resembles a cambium, but the available material was insufficient to enable the mode of secondary thickening to be fully investigated. In the vascular bundles, the xylem which is U-shaped in transverse section, surrounds the phloem on three sides (Fig. 52). The xylem and phloem are enclosed within a sclerenchymatous sheath, the cells of the outermost layer of which contain druses (cluster crystals). Xylem partly consisting of sinuous tracheids of which the ends are sometimes forked (Figs. 50, 51). The average length of the tracheids is 1·75 mm. and the maximum diameter 37μ.

Root

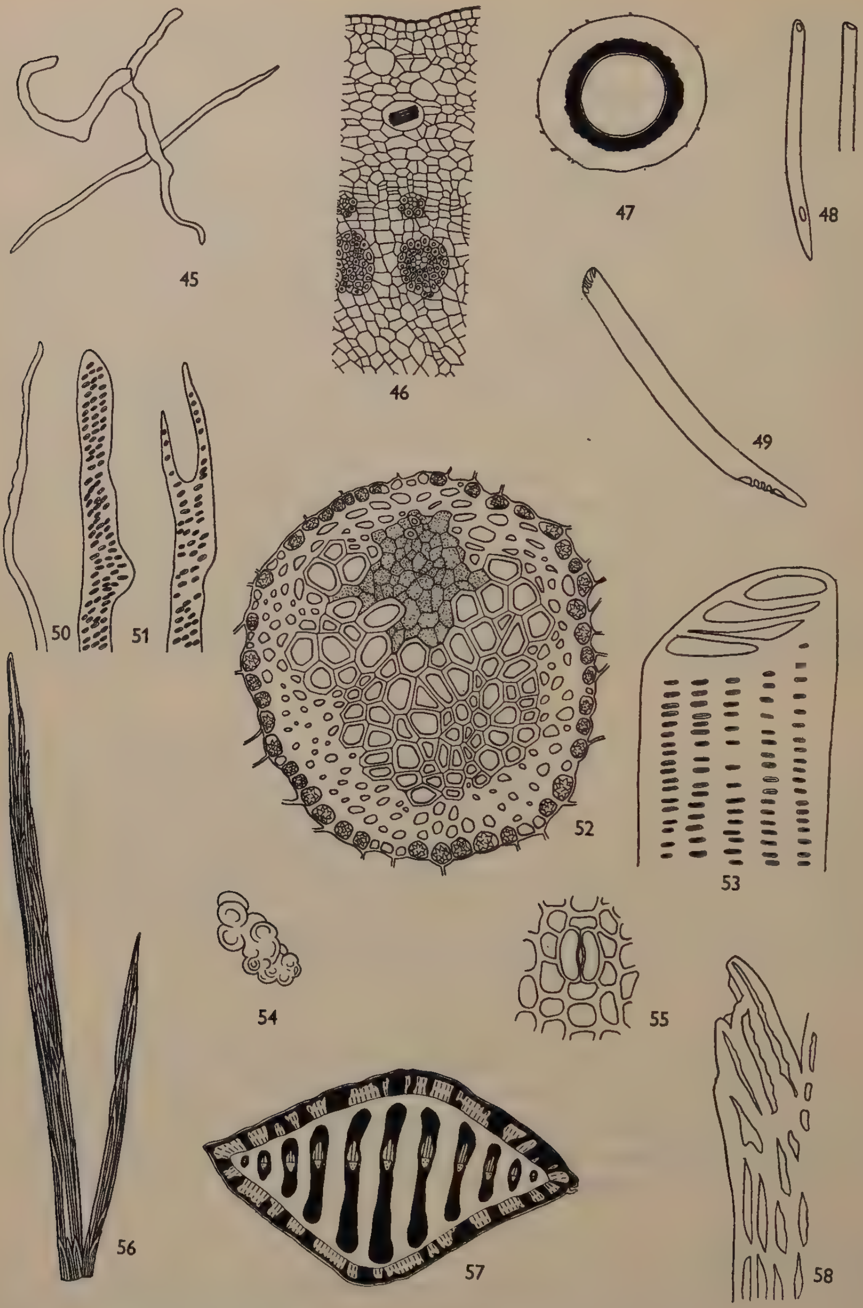
The root exhibits the following characters. A cortex consisting entirely of parenchyma; an endodermis of cells with typical U-shaped thickening; highly sclerosed cells of the pericycle and ground-tissue of the central cylinder. Xylem consisting of vessels with scalariform perforation plates (Figs. 49, 53). The length of the vessels varies from 0·7 to 1·35 mm. and their diameters from 48 to 112μ.

Material examined

Kingia australis R.Br. Kew Museum—specimen and a leaf from Morrison, 8287, Kew Herb.

(4) *Dasypogon* R.Br.

Plants each consisting of a simple stem or caudex which attains a height of many feet in old specimens of *D. hookeri* Drumm. or of several stems 15–30 cm. long, branching from a hard rhizome in *D. bromeliaefolia* R.Br. Leaves 15–30 cm. long, narrow, stiff and aggregated at the top of the stem. The broad leaf sheaths are persistent, and the scapes terminal. Two species of the genus are known.



Figs. 45–58. *Lomandra* and *Kingia*. 45. *Lomandra preissii*, rhizome tracheids, × 50. 46. *L. preissii*, T.S. rhizome, × 210. 47. *L. filiformis*, T.S. root, showing sclerenchyma (black) surrounding the endodermis, × 17. 48. *L. preissii*, vessel elements from a root, × 50. 49–58. *Kingia australis*. 49. Vessel element from a root, × 50. 50. Half of a single stem tracheid, × 50. 51. Distal parts of stem tracheids, × 210. 52. T.S. vascular bundle of the stem with a U-shaped xylem and an epithelium of cells containing druses, × 210. 53. Distal part of a vessel member from a root, × 210. 54. Sponge-like sclerosed cell from a substomatal chamber extracted by maceration, × 210. 55. Stoma with seven subsidiary cells in surface view, × 210. 56. Hairs from the base of a leaf, × 50. 57. T.S. leaf, × 17. 58. L.S. leaf margin.

Leaf

Leaf flattened and inversely bifacial (Fig. 59), the palisade tissue being confined to the abaxial side of the leaf. Epidermis consisting of cubical cells with somewhat thickened walls and a very thick cuticle, which extends over the stomatal cells. Stomata confined to the abaxial side of the leaf where they are almost at the same level as the other epidermal cells, and lead to very small substomatal chambers (Figs. 62, 70). Each stoma is surrounded by four to six subsidiary cells (Figs. 60, 61) (in *D. bromeliaefolia* the dominant number is 4, and in *D. hookeri* the numbers 5 and 6 are the most frequent). Leaf margins denticulate. In *D. hookeri* the teeth consist of parenchyma and epidermal cells similar to those of the other parts of the leaf (Fig. 64). In *D. bromeliaefolia* the teeth are stiff and more hair-like, and consist of elongated, pointed, overlapping cells with a thick cuticle (Fig. 67). In this species the epidermal cells between the teeth at the leaf margins have small cuticular papillae (Fig. 67). The photosynthetic tissue consists of three layers of palisade cells. The palisade cells, especially those of the outer layers, bear rows of papillose projections (Fig. 62). When the projections of contiguous cells are so arranged that they do not interlock, intercellular spaces are formed between the palisade cells. The part of the leaf between the palisade tissue and the adaxial epidermis consists of thick-walled parenchyma with a row of vascular bundles embedded in it. Every vascular bundle consists of a ground-tissue of fibres and three strands of xylem and phloem. In the middle of the fibrous ground tissue there is a large vascular strand and laterally two small and inconspicuous strands (Fig. 59). A single-layered parenchymatous sheath can be recognized around every vascular bundle in *D. bromeliaefolia.* Xylem consisting of long and pitted tracheids.

Rhizome

Cortex, in the rhizome of *D. bromeliaefolia*, consisting of two zones. (1) An outer part made up of the epidermis and parenchymatous cells with thickened walls. (2) An inner part composed of thin-walled parenchyma. The endodermis, as in the roots of most monocotyledons, consists of cells with U-shaped thickenings. Within the endodermis there is a pericycle consisting of many layers of sclerenchyma. The central part of the stem consists of vascular bundles embedded in a mass of parenchymatous cells with somewhat thickened walls. These cells include numerous starch grains. The vascular bundles are amphivasal, and surrounded by sclerenchymatous sheaths. Long tracheids, which in *D. bromeliaefolia* had an average length of 3·5 mm., occur in the xylem. No tracheids were seen that exceeded 22μ in diameter.

Scape

(1) *D. bromeliaefolia* (Fig. 63). The epidermis, which bears multicellular hairs with shield-like bases (Fig. 65), consists of cubical cells with a thin cuticle. The outer part of the cortex consists of small cells with chloroplasts, and the inner part of larger cells without chloroplasts. The outer part of the central cylinder is sclerosed and the inner part is made up of thick-walled parenchyma (Fig. 63). The vascular bundles are collateral and surrounded by sclerenchymatous sheaths. Long scalariform tracheids occur in the xylem, and elements with annular and spiral thickenings, believed to be from the protoxylem, have also been seen.

(2) *D. hookeri*. The structure is similar to that just described for *D. bromeliaefolia*, but the tissues in the outer part of the vascular cylinder, and around the vascular bundles, are not sclerosed, and the walls of the cells of the inner part of the vascular cylinder have thinner walls. The multicellular hairs are also smaller (Fig. 66).

Root

The following description refers to a root of *D. bromeliaefolia*, 2·5 mm. in diameter.

There are two zones in the cortex; the outer one, consisting of small cells with thickened walls; the inner one compound of large thin-walled cells. The endodermis consists of cells with typical U-shaped wall thickenings, and the pericycle of five to seven layers of large sclerified, radially flattened cells. Within the pericycle there is a zone of fibres in which the vascular bundles are embedded and in the centre of the root there is a thick-walled pith (Fig. 68). The xylem consists chiefly of vessels, with a simple perforation at either end of each element, but narrower elements, each with a simple perforation at one end and an imperforate tapering end at the other, also occur (Fig. 69). The length of the vessel elements in *D. bromeliaefolia* was found to vary from 0·5–0·9 mm., and the diameter from 48–95μ.

Material examined

D. bromeliaefolia R.Br., Morrison, 7243, Kew Herb.
D. hookeri Drumm., Kew Museum.

(5) *Chamaexeros* Benth.

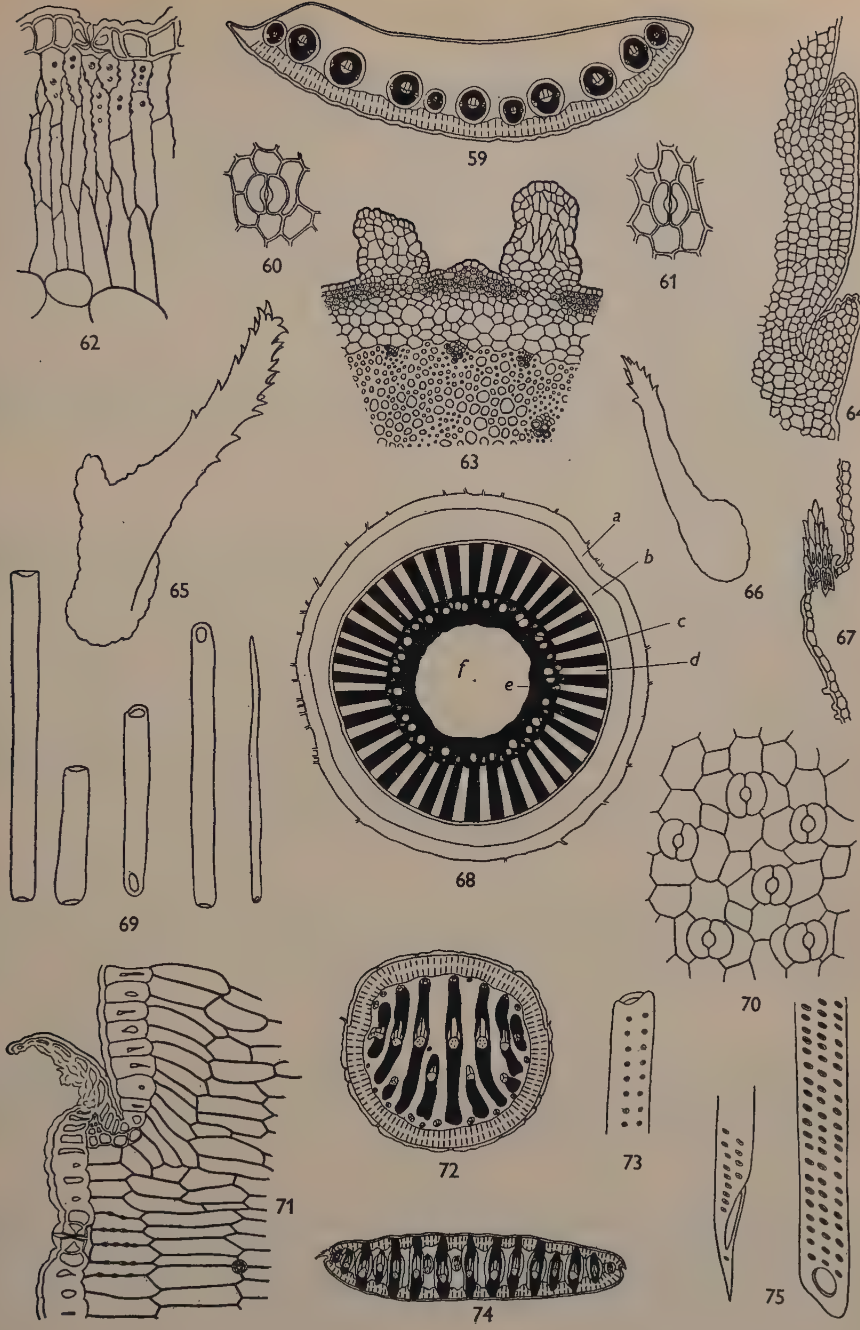
Plants consisting of short tufted stems bearing stiff linear leaves which are flat and about 15 cm. long in *C. serra*, and almost cylindrical and 30–45 cm. long in *C. fimbriata*. Only the two species mentioned above are known.

Leaf

The leaf is isolateral in both species, but this is one of the few characters that are common to both. For this reason the leaf of each species is described separately.

(1) *C. fimbriata*: leaf cylindrical (Fig. 72); epidermis consisting of almost cubical cells with very thick cell walls, except for the four to six thinner-walled subsidiary cells around each of the stomata. A somewhat thick cuticle covers the epidermal and stomatal cells. Stomata somewhat depressed below the other epidermal cells. A flattened substomatal chamber occurs below each stoma. At each lateral margin of the leaf a narrow scarious, lacerated membrane occurs. These membranes consist wholly of outgrowths of epidermal tissue (Fig. 71). The palisade tissue surrounds a pith-like, thick-walled cell mass in which the vascular bundles are embedded. It consists of three to four compact layers of palisade cells with thickened walls. Very small intercellular spaces can be seen between those palisade cells which are situated below the stomata. Rows of elongated cells lying parallel to the long axis of the leaf, and each of which contains about eight very long crystals resembling raphides (Fig. 71), occur in the palisade tissue. The vascular bundles are arranged as follows. A ring of numerous small bundles occurs immediately within the palisade tissue. A tangential row of large bundles is present just above the equatorial position in the leaf. The large bundles are embedded in well-developed I-girders of sclerenchyma of which the distal ends extend almost to the palisade tissue towards both the adaxial and abaxial surfaces of the leaf. A second tangential row of medium sized vascular bundles is developed somewhat below the equatorial plane, and more towards the abaxial surface of the leaf. Short girders of sclerenchyma also extend from these bundles almost to the abaxial palisade tissue (Fig. 72).

(2) *C. serra*. Leaf flat (Fig. 74). Epidermis consisting of two kinds of cells (i) those above the sclerenchyma bands which are relatively long and not accompanied by stomata, and (ii) shorter cells above the photosynthetic tissue between which stomata are present. The walls of the epidermal cells, except those of the four to six (mostly four) subsidiary cells around the stomata, are very thick, the outer periclinal walls being more thickened than the remainder. The cuticle is of medium thickness. Very narrow, lacerated, membranes, similar to those in *C. fimbriata*, occur at the leaf margins. Stomata somewhat



Figs. 59–75. *Dasypogon* and *Chamaexeros*. 59. *D. bromeliaefolia*, T.S. leaf, × 17. 60. *D. hookeri*, stoma surrounded by five subsidiary cells, × 210. 61. As Fig. 60 but with six subsidiary cells. 62. *D. hookeri*, T.S. leaf showing palisade tissue in the stomatal region, the upper palisade cells having papillose projections and there are small intercellular spaces between them, × 210. 63. *D. bromeliaefolia* T.S. scape showing bases of multicellular hairs, × 50. 64. *D. hookeri*, L.S. leaf margin, × 50. 65. *D. bromeliaefolia*, hair from the scape, × 50. 66. *D. hookeri*, hair from the scape, × 50. 67. *D. bromeliaefolia*, L.S. leaf margin, × 50. 68. *D. bromeliaefolia*, T.S. root, *a* and *b* = cortex, *a* = small thick-walled cells, *b* = large thin-walled cells, *c* = endodermis, *d* = pericycle, *e* = fibrous tissue in which the vascular bundles are embedded, *f* = pith, × 17. 69. *D. bromeliaefolia*, vessel elements from roots, × 50. 70. *D. bromeliaefolia*, abaxial epidermis, × 210. 71. *Chamaexeros fimbriata*, T.S. leaf, lateral part, × 210. 72. *C. fimbriata*, T.S. leaf, × 17. 73. *C. fimbriata*, distal part of a vessel element from a root, × 250. 74. *C. serra*, T.S. leaf, × 17. 75. *C. serra*, distal parts of vessel elements from a root, × 210.

raised above the remaining epidermal cells. Palisade tissue interrupted by the distal ends of the sclerenchymatous I-girders that extend from most of the vascular bundles to the adaxial and abaxial epidermis. Of the palisade cells themselves, those towards the centre of the mesophyll are shorter and contain fewer chloroplasts than those immediately below the epidermis. Besides the girders of sclerenchyma that extend from the vascular bundles in the manner just described, each vascular bundle is also accompanied laterally by a single-layered incomplete sheath of large colourless cells (Fig. 74). Long tracheids are to be seen in the xylem.

Stem

Epidermis and outer part of the cortex composed of thick-walled cells. Vascular bundles amphivasal, the xylem consisting mainly of pitted tracheids somewhat similar to those of *Xanthorrhoea minor*. Their average length in *Chamaexeros serra* measured 0·8 mm. and their maximum diameter 22μ.

Root

Inner part of the cortex consisting of a few layers of fibres. Endodermis composed of cells with typical U-shaped thickening in *C. fimbriata*, and of cells with all the walls equally thickened in *C. serra*. Pericycle consisting of one layer of thick-walled cells, somewhat smaller than those of the endodermis. Pith composed of thick-walled cells. Xylem partly consisting of vessels of which the elements have simple perforations, but in *C. serra* the perforation plates have been seen to be oblique, and the ends of the vessel elements sometimes taper to points (Fig. 75). In *C. fimbriata* the perforation plates are more transverse (Fig. 73). The length of the vessel elements in *C. serra* was found to vary from 0·83 to 1·50 mm. and the diameter from 20 to 80μ. In *C. fimbriata* the length varies from 0·816 to 1·680 mm. and the diamter from 22 to 27μ.

Material examined

C. fimbriata (F. Muell.) Benth., E. Lankaster, 4 September 1887 (Herb. Morrison) Kew Herb.

C. serra (Endl.) Benth., Morrison, 12203, Kew Herb.

(6) *Calectasia* R.Br.

Plants consisting of a rhizome bearing branched aerial stems which are mostly about 30 cm. high. Leaves short and linear. One species of the genus has already been recognized and a second still awaits description.

Leaf

Leaf isolateral and somewhat V-shaped in transverse section (Fig. 78). Epidermis consisting of large, more or less cubical cells with thickened walls and large lumina. A very thick cuticle covers the epidermal and the stomatal cells. The stomata, each of which is surrounded by five to six (sometimes four) subsidiary cells are somewhat raised above the other epidermal cells (Figs. 76, 77, 79 and 83). The substomatal chambers are large. Hairs are of two kinds. (i) Branched multicellular uniseriate hairs, the distal ends of each cell tapering to a point and outwardly directed (Fig. 80). Hairs of this kind occur at the margins of the sheath and lamina in *Calectasia* n.sp., but in *C. cyanea* they are confined to the margins of the sheath. (ii) Acutely pointed, unicellular hairs, each resembling a single constituent cell of one of the multicellular hairs just described, occur on the abaxial surface of the leaf of *Calectasia* n.sp. and at the margins of the lamina of *C. cyanea*. A single layer of palisade tissue surrounds a small pith-like mass of large thick-walled parenchyma cells. The palisade cells, which are large and thick-walled, are of two kinds and similar to those of *Kingia*. The first type is provided with papillae arranged in longitudinal rows, and the second is characterized by annular constrictions in which low papillae can also be seen. Intercellular spaces are formed between adjacent cells of the first type if the papillae do not interlock.

Rounded or elliptical intercellular spaces are always present between cells of the second type. The central, pith-like cells of the mesophyll, between which there are small intercellular spaces, superficially resembling bordered pits, have their long axes in the same plane as the longer transverse axis of the leaf. Raphide cells, lying parallel to the long axis of the leaf, occur amongst the pith-like cells that have just been described.

Three vascular bundles, each sheathed by a single layer of parenchyma, are embedded in the colourless central mesophyll. Every bundle consists of a ground-tissue of fibres embedded in which there are two small, lateral, and one larger median, strands of conducting tissue (Fig. 78). Short tracheids occur in the xylem.

Stem

Epidermis and cortex compound of thin-walled cells. Small groups of sclerenchyma sometimes occur below the epidermis. The endodermis, consisting of lignified cells, encircles a cylinder of fibres which, in turn, surrounds a thick-walled parenchyma in the centre of the stem. Vascular bundles amphivasal. Very long, pitted tracheids occur in the xylem. The average length of those in *C. cyanea* measured 6 mm. and the maximum diameter 23μ.

Root

Cortex wholly parenchymatous. Endodermis consisting of cells of which all the walls are equally thickened. Central cylinder completely sclerified. The pericycle in *C. cyanea* consists of four to five layers of wide sclerenchymatous cells, and in *Calectasia* n.sp. of only two layers of typical fibres. Xylem including vessel elements with simple transverse or oblique perforations. In *C. cyanea* the large vessels are wider than those of *Calectasia* n.sp. The xylem, besides the typical vessel elements mentioned above, also includes elements with one end perforated and the other closed as in a tracheid, together with typical small tracheids (Figs. 81, 82 and 84). The vessel elements of *C. cyanea* are 0·55–0·88 mm. long and $28–72\mu$ in diameter, and those of *Calectasia* n.sp. 0·480–0·800 mm. long and $28–37\mu$ in diameter.

Material examined

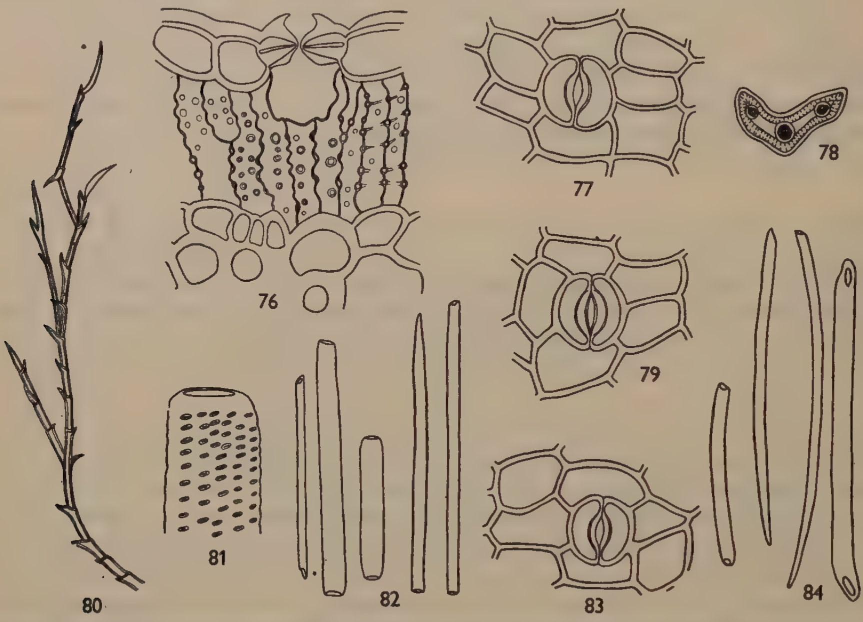
C. cyanea R.Br. Morrison, 7248 and 7244, Kew Herb.
Calectasia sp. nov. Morrison, 16165, Kew Herb.

(7) *Baxteria* R.Br.

The sole species consists of a short woody rhizome which bears tufts of linear leaves which are 30–45 cm. long and have sheath-like bases. Flowers solitary, arising in the middle of the radical leaves.

Leaf

Leaf isolateral. Its shape in cross-section is a flattened rhombus (Fig. 86). Epidermis composed of somewhat elongated cells. Those above the bands of perivascular sclerenchyma being slightly more elongated in the direction of the long axis of the leaf than those above the chlorenchyma. The walls of the epidermal cells are very little thickened. A fairly thick cuticle covers the epidermal cells apart from the subsidiary and guard cells of the stomata. The stomata, each of which is surrounded by four subsidiary cells, are somewhat depressed below the other epidermal cells. Druses occur in all the epidermal cells above the bands of perivascular sclerenchyma (Fig. 89), but are only occasional in the other epidermal cells. Flat teeth (Fig. 85), each consisting of very thick-walled cells and covered by a very thick cuticle, occur at the leaf margins. Hypodermis consisting of sclereids. The substomatal chambers are lined by peculiar, twisted, sponge-like, sclerosed cells with many papillose projections (Fig. 87). The photosynthetic tissue consists of short palisade cells, whilst there is a gradual transition to isodiametric cells towards the centre of the mesophyll. Some small, rounded, intercellular spaces occur between the cells of the photosynthetic tissue.



Figs. 76–84. *Calectasia*. 76. *Calectasia* n.sp., T.S. leaf, showing palisade tissue in the stomatal region; palisade cells with papillose projections and typical intercellular spaces, × 210. 77. *C. cyanea*, stoma surrounded by six subsidiary cells, × 210. 78. *C. cyanea*, T.S. leaf, × 17. 79. *C. cyanea*, stoma with five subsidiary cells, × 210. 80. *Calectasia* n.sp., hair from leaf margin, × 50. 81. *C. cyanea*, distal part of a vessel member from a root, × 210. 82. *C. cyanea*, vessel elements from a root, × 50. 83. *C. cyanea*, stoma with four subsidiary cells, × 210. 84. *Calectasia* n.sp., vessel elements from a root, × 50.

Every vascular bundle is embedded in sclerenchyma and surrounded by a one-layered sheath of large parenchyma cells without chloroplasts. These bundles are connected to the adaxial and abaxial epidermis by bands of sclerenchyma (Fig. 86). Long tracheids occur in the xylem.

Rhizome

Vascular bundles amphivasal. The xylem consists of sinuous tracheids, which are 1·2–2·8 mm. long and have a maximum diameter of 37 μ.

Root

Cortex wholly parenchymatous. Endodermis consisting of cells with typical U-shaped wall thickenings. Pericycle consisting of one layer of thick-walled cells with conspicuous lumina. Centre occupied by a large pith consisting of thick-walled cells. Xylem including vessels with oblique, scalariform perforations. Elements of the large vessels 1 × 0·1–1·8 × 0·1 mm.; smaller vessels about 1 × 0·06 mm. Very narrow elements about 1·4 × 0·015–1·7 × 0·03 mm. also occur. It was not possible to determine with certainty whether these narrow elements should be interpreted as vessel elements with very oblique perforation plates, or as tracheids.

Material examined

B. australis R.Br., Kew Museum.

(8) *Acanthocarpus* Lehm.

The sole species consists of a rigid but rather slender stem bearing numerous, short, divaricate branches forming either dense tufts 15–30 cm. long or a straggling shrub of 30–60 cm. Leaves linear, rigid, subulate to almost lanceolate, 1·5–5 cm. long.

Leaf

Leaf isolateral, flattened; adaxial surface slightly concave; abaxial surface convex or rounded; grooves present in all surfaces (Fig. 90). Epidermis in the strips above the perivascular sclerenchyma bands consisting of cells that are considerably elongated in the same direction as the long axis of the leaf. The cells above the alternating strips of the palisade tissue are somewhat shorter. The walls of the epidermis are thick. The cuticle is even thicker than elsewhere on the surface of the large papillae, which are described below. Epidermal outgrowths of two kinds: (i) Rows of papillae, which are either solitary or in small groups, occur on both sides of the furrows in which the palisade tissue is situated. The papillae serve for the protection of the stomata (Fig. 98). (ii) Small scale-like structures (Figs. 92, 93) occur at the leaf margins. Each of these consist of a few epidermal cells, protruding considerably from the surface of the leaf. Each stoma is surrounded by four or sometimes five, subsidiary cells. The photosynthetic tissue, which consists of two to three layers of short palisade cells, is interrupted by the distal ends of the bands of perivascular sclerenchyma which reach the adaxial and abaxial epidermis. The intercellular spaces between the palisade cells, especially in the region of the stomata, are similar to those that have already been described in *Kingia* and *Calectasia*, but they are much less well developed. Parenchyma cells with only a few chloroplasts occur between the palisade cells below both surfaces of the leaf. Cells containing raphides can sometimes be seen in this tissue. The vascular bundles are accompanied by one-layered sheaths of very large cells without chloroplasts. Xylem including vessels of which the elements have very oblique scalariform perforation plates.

Stem

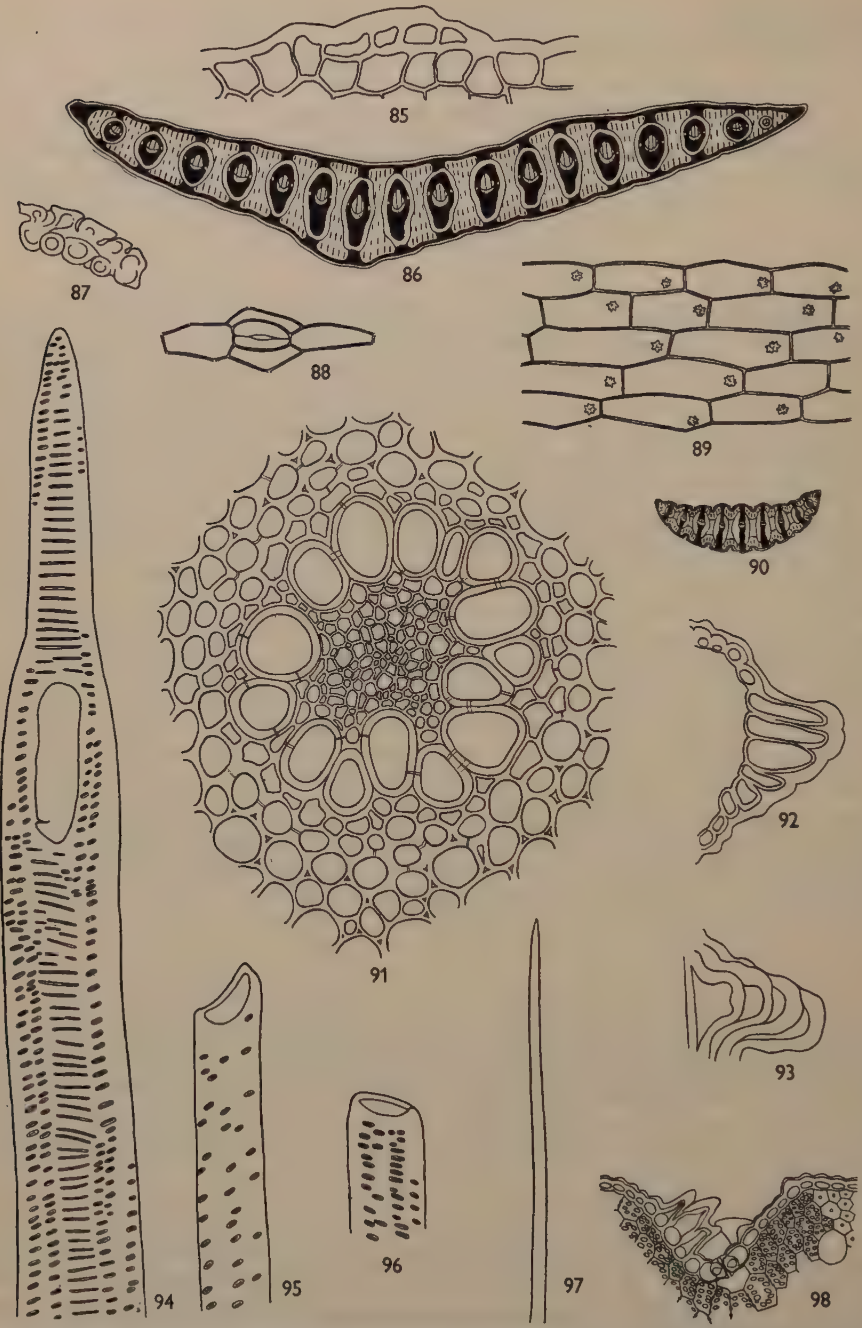
Epidermis resembling collenchyma, and covered by a thick cuticle. Below the epidermis there is a zone of about ten layers of parenchyma cells between which a number of specially large cells containing raphides were noted. The central cylinder consists of an outer zone of six to eight layers of fibres surrounding a large central mass of thick-walled parenchyma. The vascular bundles are amphivasal (Fig. 91). Xylem including tracheids as much as 6 mm. or more long and with a maximum diameter of 37μ (Fig. 97).

Root

Inner part of the cortex consisting of a zone of a few layers of sclerenchymatous cells. Endodermis consisting of cells with all the walls equally thickened. Pericycle one-layered. Pith consisting of a thick-walled parenchyma. Xylem including large vessels of which the elements have simple, usually transverse but more rarely oblique, perforations (Figs. 94–96). The vessels are 0·960–2·480 mm. long and 16–80μ in diameter.

Material examined

A. preissii Lehm. var. 1, Morrison, 15140, Kew Herb.
A. preissii Lehm. var. 2, Morrison, 10217, Kew Herb.



Figs. 85–98. *Baxteria* and *Acanthocarpus*. 85–89. *Baxteria australis*. 85. L.S. leaf margin, × 210. 86. T.S. leaf, × 17. 87. A sponge-like sclereid extracted by maceration from a substomatal chamber of the leaf, × 210. 88. Stoma with four subsidiary cells, × 210. 89. Epidermal cells, from above the vascular bundles of the leaf, containing druses, × 210. Figs. 90–98. *Acanthocarpus preissii*. 90. T.S. leaf, × 17. 91. T.S. an amphivasal vascular bundle of the stem, × 210. 92. T.S. hair at leaf margin, × 210. 93. As Fig. 92 but in surface view, × 210. 94–96. Vessel elements from a root, × 210. 97. One-fifth of a stem tracheid, × 50. 98. T.S. leaf, passing through the stomatal region, × 210.

Table 1

(+ elements present; — elements absent; . organs not examined)

Species	Tracheid (mm.)	Vessel with scalariform perforation	Vessel with simple perforation	Tracheid (mm.)	Vessel with scalariform perforation (mm.)	Vessel with simple perforation (mm.)
		Leaf			Stem	
canthocarpus preissii Lehm.	—	+	—	6·0 × 0·037	—	—
axteria australis R.Br.	+	—	—	.	.	.
alectasia cyanea R.Br.	+	—	—	6·0 × 0·023	—	—
alectasia n.sp.	+	—	—	+	—	—
hamaexeros fimbriatus (F. Muell.) Benth.	+	—	—	.	.	.
. serra (Endl.) Benth.	+	—	—	0·8 × 0·022	—	—
asypogon bromeliaefolia R.Br.	+	—	—	.	.	.
. hookeri Drumm.	+	—	—	.	.	.
ingia australis R.Br.	+	—	—	1·75 × 0·037	—	—
omandra confertifolia (T. M. Bail.) Fahn	+	—	—	2·0–2·72 × 0·016–0·019	—	—
. preissii (Endl.) Ewart	+	—	—	.	.	.
. endlicheri (F. Muell.) Ewart	+	—	—	.	.	.
anthorrhoea minor R.Br.	—	+	—	1·0–3·0 × 0·030	—	—
. australis R.Br.	—	+	—	.	.	.
		Rhizome			Root	
canthocarpus preissii Lehm.	.	.	.	—	—	0·96–2·48 × 0·016–0·080
axteria australis R.Br.	1·2–2·8 × 0·037	—	—	—	1·0–1·8 × 0·016–0·1	—
alectasia cyanea R.Br.	.	.	.	—	—	0·55–0·88 × 0·028–0·072*
alectasia n.sp.	.	.	.	Sometimes	—	0·48–0·8 × 0·028–0·037*
hamaexeros fimbriata (F. Muell.) Benth.	.	.	.	—	—	0·816–1·68 × 0·022–0·027
. serra (Endl.) Benth.	.	.	.	—	—	0·83–1·5 × 0·02–0·08
asypogon bromeliaefolia R.Br.	3·5 × 0·022	—	—	—	—	0·5–0·9 × 0·048–0·095*
. hookeri Drumm.	.	.	.	—	—	+*
ingia australis R.Br.	.	.	.	—	0·7–1·35 × 0·048–0·112	—
omandra confertifolia (T. M. Bail.) Fahn	.	.	.	—	—	+
. preissii (Endl.) Ewart	0·8 × 0·022	—	—	—	—	1·04–1·7 × 0·032
. endlicheri (F. Muell.) Ewart	.	.	.	—	—	+
anthorrhoea minor R.Br.	.	.	.	—	—	0·96–1·28 × 0·037–0·056
. australis R.Br.	.	.	.	.	.	.

* Elements with one end perforated and the other closed, as in tracheids, also occur here.

Dimensions of the vascular elements

It is now generally accepted by plant anatomists that the morphology and lengths of the tracheal elements give some indication of the phylogenetic status of the plants in which they are exemplified. Thus the tracheid is believed to be ancestral to the vessel element, and long vessel elements with scalariform perforation plates are believed to have given rise to shorter elements with simple perforations. Modern views on this subject have been summarized by Metcalfe & Chalk (1950). The data that have been collected during the present investigation concerning the form and dimensions of the tracheal elements are summarized in Table 1 for the convenience of students of phylogeny. The numerical data in the table are based on a restricted number of measurements in a limited amount of material, for which reason it is inadvisable to place too much reliance on them when drawing phylogenetic conclusions. Nevertheless, it is hoped that they will serve as a basis for making comparisons with other monocotyledons, including many that still await investigation. It is believed that the qualitative morphological differences between the different types of tracheal cell are less variable than are the dimensions of the cells, for which reason they are more reliable as indicators of phylogenetic status.

Discussion

(1) *Taxonomic and phylogenetic conclusions to be drawn from the anatomical evidence*

Bentham and Hooker included the genera described in this paper in the Juncaceae as the tribes Xeroteae and Calectasieae. Engler included them in the Liliaceae under the tribes Dasypogoneae, Lomandreae and Calectasieae. Hutchinson (1934), following Dumortier but with some modifications, regards them as a separate family of plants that may well represent 'very advanced members of the Liliaceous stock, and something of a parallel to part of the Agavaceae, but tending towards the habit and unisexualism of the Palmae'.

The facts revealed by the anatomical examination appear to support Hutchinson's opinion, although the available anatomical data concerning the Juncaceae and Liliaceae are as yet insufficient to enable a final conclusion to be drawn.

That the Xanthorrhoeaceae is a much less advanced family than the Juncaceae can be seen from the fact that, while vessels occur in all organs of the plant (Cheadle, 1942) in the Juncaceae, they are nearly always confined to the roots in the Xanthorrhoeaceae. Cells which are probably true vessel elements were, however, found in the leaves of *Xanthorrhoea* and *Acanthocarpus*. According to Cheadle (1942) most of the forty-three species of Liliaceae which he examined have vessels only in the roots, and the perforation plates in the vessel members are generally scalariform. In the Xanthorrhoeaceae, on the other hand, the root vessels exhibit simple perforations in six out of the total of eight genera, scalariform plates being confined to the remaining two. On the evidence provided by the distribution and structure of the vessels the Agavaceae appear to resemble the Xanthorrhoeaceae more closely than does any other family. As in the Xanthorrhoeaceae, so in the Agavaceae, the vessels, which are almost wholly confined to the roots, mostly exhibit simple perforations. It is interesting to note, however, that just as vessels in the leaves occur only in *Xanthorrhoea* and *Acanthocarpus* amongst the Xanthorrhoeaceae, so are leaf vessels restricted to *Cordyline* and *Dracaena* amongst the Agavaceae. Where vessels occur in the leaves of the four genera just mentioned they are always provided with scalariform perforation plates.

The vascular bundles that exhibit two groups of phloem and a V-shaped xylem and which occur in the leaves of *Xanthorrhoea* are very similar to those of *Dasylirion acrotrichum* (Kny, 1881) of the Agavaceae.

Neither the tribes Xeroteae (including *Lomandra* (*Xerotes*), *Chamaexeros*, *Acanthocarpus*, *Xanthorrhoea* and *Dasypogon*) and Calectasieae (including *Kingia*, *Baxteria* and *Calectasia*) as given by Bentham and Hooker, nor the Dasypogoneae (including *Dasypogon*), Lomandreae (including *Acanthocarpus*, *Chamaexeros*, *Lomandra* and *Xanthorrhoea*) and Calectasieae (including *Kingia*, *Baxteria* and *Calectasia*) as understood by Engler appear to correspond to the four taxonomic subdivisions of the family suggested by the anatomical structure.

(*a*) *The* Kingia *group consisting of* Kingia *and* Baxteria

In this group the vascular bundles of the leaves are seen to be arranged in a horizontal row when viewed in transverse sections. Immediately below the epidermis there is a hypodermis of sclereids similar to that which also occurs in *Xanthorrhoea* but in no other genus outside the *Kingia* group.

Sclereids of a curious, twisted, sponge-like type with many projections occur below the stomata, whilst druses are present in the epidermal cells. It is also noteworthy that *Kingia* and *Baxteria* are the only genera of the Xanthorrhoeaceae in which the vessels in the roots are provided with scalariform perforation plates. This fact appears to indicate that *Kingia* and *Baxteria* are the most primitive genera within the family.

(*b*) *The* Dasypogon *group, consisting of* Dasypogon *and* Calectasia

Although the leaves of *Dasypogon* have palisade tissue only towards the abaxial surface and therefore differ from those of *Calectasia* which are isolateral, there are many other characters that are common to the two genera. The vascular bundles of the leaves are arranged in a single horizontal row, as seen in transverse sections, and embedded in a tissue of colourless parenchymatous cells. Each bundle is surrounded by a one-layered parenchymatous sheath. Every bundle consists of a mass of sclerenchyma in which three strands of phloem and xylem are included, the median vascular strand being the largest. The number of subsidiary cells around each stoma varies from four to six in both genera.

The tracheal cells in the roots of *Dasypogon* and *Calectasia* consist mostly of vessel elements with simple perforations. Besides these, however, elements that are perforated at one end, but which resemble tracheids at the other, have also been observed in both genera, whilst in *Calectasia* typical tracheids also occur.

(*c*) *The* Lomandra *group, consisting of* Lomandra, Acanthocarpus *and* Chamaexeros

There is no sclerosed hypodermis in the leaves of members of this group. The distal ends of all or part of the fascicular girders of sclerenchyma extend to the epidermis on both surfaces of the leaf except in *Chamaexeros fimbriata*, *Lomandra pauciflora* and *L. turbinata*. Cells containing raphides or similar crystals occur in the mesophyll of all members of this group; and similar cells are also to be seen in *Calectasia*, which appears, on other anatomical grounds, to be more closely related to *Dasypogon*. It should also be noted that *Acanthocarpus* and *Chamaexeros*, together with *Xanthorrhoea* of group 4 (see below), are the only genera in which there is a sclerenchymatous zone outside the endodermis in the roots.

(*d*) *The* Xanthorrhoea *group consisting of only the one genus*

The leaves in members of this group have a 'cortex' surrounding a pith-like cell-mass in which the vascular bundles are distributed, just as they are in a monocotyledonous stem. Each vascular bundle of the leaves exhibits two strands of phloem and a V-shaped xylem in transverse section.

In order to ascertain if, or to what extent, the taxonomic group of the genera that seems desirable in the light of the anatomical evidence agrees with that based on the evidence of pollen morphology, I have compared the opinions I have expressed above with those given by Erdtman in his *Pollen Morphology and Plant Taxonomy* (1952). In this book, Erdtman arranges the genera of Xanthorrhoeaceae that he examined in the following groups: (i) Dasypogoneae consisting only of *Dasypogon*; (ii) Lomandreae consisting of *Acanthocarpus*, *Chamaexeros* and *Lomandra*; (iii) Calectasieae consisting of *Calectasia* and *Kingia*. When these groups of Erdtman's are compared with those that I have proposed on anatomical grounds, it will be noted that the *Lomandra* group is composed of the same three genera—*Lomandra*, *Acanthocarpus* and *Chamaexeros*—in both classifications. Although *Calectasia* and *Kingia* have some anatomical characters that are common to both genera, the anatomical differences between the two genera appear to be more significant than the resemblances. So far as these two genera are concerned, therefore, the evidence based on pollen morphology does not point to the same conclusion as the evidence based on the general structure of the vegetative organs.

(2) *Anatomical structure in relation to the ecology of the family*

The leaves of all the species of Xanthorrhoeaceae that have been examined have a pronounced xeromorphic structure, but the extent to which the xeromorphic characters are developed varies from species to species. All of the species exhibit: (i) an epidermis of more or less thick-walled cells; (ii) a thick cuticle which covers the guard cells of the stomata as well as the other epidermal cells; (iii) a compact photosynthetic tissue consisting of cells of which the walls are somewhat thickened; (iv) a considerable development of sclerenchymatous tissue; (v) a thick-walled colourless parenchymatous region in the mesophyll of most species.

The most marked xeromorphic structure occurs in *Xanthorrhoea*, *Kingia* and *Baxteria* where the hypodermis is sclerenchymatous and the substomatal chambers are lined with special sclerosed sponge-like cells or by projections of the hypodermal sclereids. Similar papillose projections of hypodermal cells surrounding the substomatal chambers can be seen in *Guzmania monostachya* and some other species of the Bromeliaceae (Solereder & Meyer, 1929). *Calectasia* and *Dasypogon* show the least pronounced xeromorphic characters, but the leaves are, nevertheless, adequately protected against dry conditions. The leaves in these genera have an epidermis of which the cell walls are only slightly thickened, and the sclerenchyma does not extend outwards as far as the epidermis. On the other hand, the cuticle is very thick, and the palisade tissue very compact. In *Calectasia* the large cells of the epidermis look as if they might serve for the storage of water.

Xeromorphism, like other biological specializations, varies in extent and is achieved by different methods. This fact is shown, for example, in the stomatal region in different species of *Xanthorrhoea*. In *X. arborea*, *X. semiplana* and *X. bracteata* the stomata are at the same level as the other epidermal cells, and below the stomata there are projections from the sclereids of the hypodermis, which protect the small substomatal chambers against excessive evaporation (Figs. 1, 4). In *X. minor*, *X. australis*, *X. hastile* and *X. brevistyla* the stomata are slightly sunken and the substomatal chambers are lined with projections from the sclereids or by special sclerosed sponge-like cells (Fig. 3). In *X. preissii* and *Xanthorrhoea* sp. aff. *X. reflexa* the epidermal cells surrounding the somewhat sunken stomata are provided with small papillae, whilst the somewhat larger substomatal chambers are again lined with sclerosed sponge-like cells (Figs. 5, 8). Finally, in *X. gracilis* and *X. macronema*, the stomata, which are situated in furrows, are protected externally by a covering of large papillae, whilst in the substomatal chambers, which are larger than those of the species already mentioned, there are neither sclerosed sponge-like cells nor projections from the adjacent sclereids (Figs. 6, 9). The xeromorphic structures that appear to be specially characteristic of the Xanthorrhoeaceae are as follows: (i) the sclerosed twisted, sponge-like cells, that occur below the stomata in *Kingia*, *Baxteria* and some species of *Xanthorrhoea*; (ii) the projections from the hypodermal sclereids which, as already stated, surround, and extend into, the substomatal chambers in many species of *Xanthorrhoea*; (iii) the annular contractions and/or papillose projections from the palisade cells. These are sometimes so arranged, that they interlock and knit the cells together to form an interwoven mass, but elsewhere the projections from adjacent cells are opposite each other and in consequence small intercellular spaces are formed between the palisade cells. Palisade cells with prominent papillose projections occur in *Kingia*, *Calectasia*, almost all the species of *Lomandra*, and to some extent, in *Dasypogon* (Figs. 36, 62 and 76), but only traces of this type of structure are to be seen in the other genera of the family. Similar palisade cells but with their longer axis parallel to the longer axis of the leaf appear in some species of *Xyris* (family Xyridaceae). It is interesting, however, to mention that this type of palisade cells occurs especially in the Australian species of *Xyris* (Solereder & Meyer, 1929).

SUMMARY

The anatomical structure of different plant organs of nearly all the species of the eight genera of the Xanthorrhoeaceae has been described. The xylem elements of representative species of all the genera have been investigated in macerated material. True vessels have been found in the roots of all the genera, and in the leaves of *Xanthorrhoea* and *Acanthocarpus*. No tracheal elements except tracheids have been seen in the leaves of the other genera, or in the stems or rhizomes of all the genera. When these data are compared with those established by Cheadle (1942) for other families of the monocotyledons, it will be seen that the Xanthorrhoeaceae most closely resemble the Agavaceae. Amphivasal vascular bundles occur in the stems and/or rhizomes of all the genera except *Kingia* where the xylem in all the bundles is U-shaped in transverse section. The stem structure of *Xanthorrhoea* provides evidence that the amphivasal type structure has arisen by the fusion of pairs of bundles with U-shaped xylem. The leaves of all the genera have a xeromorphic anatomical structure. Special arrangements and structures, which prevent excessive evaporation occur in the stomatal regions in *Xanthorrhoea*, *Kingia* and *Baxteria*. A special type of palisade cell with annular contractions, and/or with papillose projections, occurs in *Kingia*, *Calectasia*, *Lomandra* and to a lesser extent in *Dasypogon*, and traces of this type of structure are also to be seen in the other genera of the family.

ACKNOWLEDGEMENTS

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* This article was not seen until after this paper had gone to press.

The origin of the early European potato. By Dr REDCLIFFE SALAMAN, F.R.S.

(With 5 Text-figures)

[Read 6 May 1954]

The present communication may be regarded both as a continuation of the arguments presented by its two predecessors, Salaman (1946), and Salaman & Hawkes (1949), as well as a further step towards the solution of the problem raised by Bukasov (1930) and his colleagues when they made the statement that 'From the mountainous center in the Andes, the Chiloean center on the south coast where *S. tuberosum* sens. str. the ancestor of all our commercial varieties took its origin, must be separated'. The suggestion being that the place of origin and habitat of the original *Solanum tuberosum*, sensu stricto was confined to the Island of Chiloe and the neighbouring coastal area of the mainland. In short, that so far from our domestic potato being the product of a wild ancestor born in the valleys or great plateaus of the Andean Sierra, cultivated in the pre-Inca and Inca Empire of Peru and ultimately removed thence to Europe, it arose in the lowlands of Chile and Chiloe between the latitudes of S. 41° and S. 43°, and from thence reached Europe.

The 1944 paper dealt with the problem on taxonomic grounds and demonstrated that there was abundant evidence to show that our European potato might well have been derived from one of several *S. andigenum* varieties, the like of which are to-day cultivated in Northern Peru, Ecuador and Colombia. In this same paper the formidable historical argument against a Chilean origin, which had been formulated by myself in 1937, was set forth in detail.

In the 1949 communication the antiquarian argument in favour of an *S. andigenum* origin was developed. The argument was based on the unequivocal evidence derived from the study of a series of some twenty herbarium specimens of the potato, introduced to or cultivated in England and Western Europe during the seventeenth and eighteenth centuries. The series begins with a preparation left us by Gaspard Bauhin himself which may refer to the description of the potato which he published in his Phytopinax in 1596 and continues with others culled from collections ranging throughout the seventeenth and the first half of the eighteenth centuries. In these records the evolution of our domestic potato from a typical *S. andigenum* type can be followed step by step.

Collateral support was derived from the woodcuts of the potato to be found in contemporary Herbals and in particular from a charming aquatint in the Plantin Museum in Antwerp, which depicts the type potato plant received by Clusius and distributed by him throughout Western and Central Europe.

Thanks to Dr K. O. Müller I have lately come into possession of material from Chile, consisting of a number of leaves of Chilean potato varieties gathered and dried by him in the year 1952.

Leaves from twenty-six individual plants were collected in the Chiloe province, viz. between latitudes 41 and 43, and three others were plucked in the neighbourhood of La Serena, lat. S. 30°. These latter have exceptionally low leaf indices, viz. 45, 53, and 55, and are typical examples of *S. andigenum* group III (R.N.S. 1944).

I have further had the opportunity of studying seedling families raised from natural seed balls gathered by Dr Müller in the province of Chiloe. The resulting families were raised in the trial grounds of the Scottish Plant Breeding Station at Corstorphine. I am indebted to Dr William Black who raised the families, to Dr J. E. Gregor, the Director of the Station for permission to use this material, and not least to Mr J. W. Dunnett who prepared and forwarded the same to me from Edinburgh.

In the study of the series of *S. andigenum* types brought to England by Dr Hawkes from South America in 1939, I made use of a simple mathematical relation for the elucidation of differences in leaf shape which would have otherwise been difficult to define in words. The ratio A/B where 'A' represented the length of the second lateral leaflet from the distal end of the rachis of a full grown leaf, and 'B' the distance between the first distal node on the leaf rachis and the fourth. This ratio when taken to the nearest whole number was spoken of as the 'Leaf Index'.

With the use of this device I was able to show that whilst there was a wide range of variation in the species *S. andigenum* throughout the Andean regions from Colombia in the north to Jujuy in Argentina in the south, there was, nevertheless, a certain definite pattern to be observed in the distribution of the subvarieties when classified on the basis of their leaf character. Plants with the longest and narrowest leaves, built up of relatively narrow leaflets widely spaced on the rachis, i.e. plants with low foliar indices, occurred in increasing proportion in the local collections as the site of these was removed southwards from Colombia and approached the Cuzco region. Northward from Cuzco the potato varieties tended to exhibit a steadily increasing proportion of plants bearing broader, more condensed leaves, and hence exhibiting higher leaf indices. In short, *S. andigenum* types occurred in the northern area of South America which were increasingly akin in leaf character and habit of growth to our home-grown domestic types.

The Chilean material in my possession is neither sufficiently extensive nor adequately representative to enable a like generalization to be made with any assurance. The striking difference, however, between the three specimens from La Serena, lat. S. 30, and those from the Chiloe area suggests that a similar though directionally inverse differentiation in respect to leaf shape has taken place to the south of Cuzco as was evident to the north of it.

A review of the Chilean material examined in terms of leaf types and groups as described in my 1944 paper is rewarding. The extensive material collected by J. G. Hawkes and his colleagues was classified on the basis of leaf type in six groups. The fifth group contained those plants whose leaves in shape, size and structure were more or less identical with that of our domestic varieties, whilst the stems, by reason of their number and slender build, adhered to the common *S. andigenum* type.

The sixth group comprised plants with a group V leaf borne on stouter and fewer stems; such plants were in fact very similar to if not identical with many of our domestic European varieties. In the Chilean series the available data allows only of a classification into groups I–V.

That is to say that group V contain not only its own members but also any that might, had we more information, have been included in group VI.

The material gathered in the province of Chiloe comprises twenty-seven plants and they are distributed as follows: group I, 51·8%; group II, 25·9%; group III, 3·3%; group IV, 7·4%; group V, 11·1%.

If we contrast groups I–III inclusive with groups IV–V, the ratio is 81:19. That is, there are over four times as many cultivated domestic potato plants bearing outspoken *S. andigenum* characteristics in the Chiloe district as there are those akin to the European domestic type which has been given the name of *S. tuberosum*.

We may contrast these figures with the comparable ones occurring in the Colombian section of Hawkes's 1939 Potato Collection, in which the ratio was twenty-seven outstanding *S. andigenum* plants to sixty-four more or less completely domestic, i.e. *S. tuberosum* in type.

It would appear that the chances of finding a cultivated potato akin to *S. tuberosum* type in Colombia is nearly three times as great as it would be in the Chiloe area over 3000 miles farther south. It is, however, not suggested that this is a convincing argument against a possible Chilean origin.

The Spanish city of Cartagena on the coast of Colombia was the exit port for the Spanish galleons returning to Spain, and it may be confidently believed that it was by their means that potatoes taken aboard as cook's stores eventually reached Spain. It was from Cartagena that Drake in 1585 restocked his ships. Moreover it was on his journey home that he took off Harriot and his companions from Roanoke in North America. Harriot had made a collection of the plants growing in Virginia and brought the same back to England. It is permissible to suppose that when he found that a new kind of tuberous plant food was being used in the cook's galley that he added some of the tubers to the collection, which he gave to Gerard. This would explain how it came about that Gerard, whilst declaring that the potato (*S. tuberosum*) came from Virginia, nevertheless referred to it by the name it had acquired in Peru, viz. '*Papus*'.

This, however, is not to say that introductions other than those described by Clusius and Gerard, if indeed there were such, must necessarily have been like them, typical examples of *S. andigenum*. All that is claimed is that the province of Chiloe has no advantage whatever in respect to its indigenous cultivated potatoes which would entitle it to be considered the most likely place of origin of our domestic potato. It should always be remembered that the difficulties to be encountered in bringing tubers from Chile at the appropriate time were overwhelmingly greater than those which actually occurred in the transport of tubers from Cartagena.

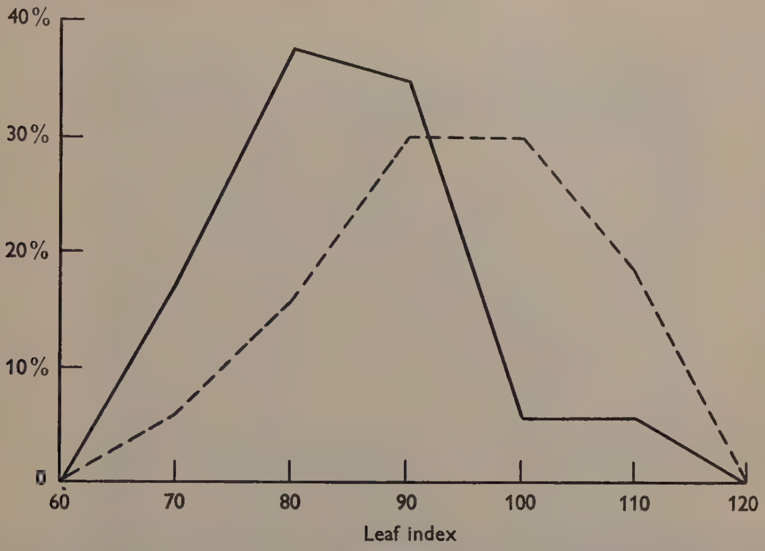

Fig. 1. The continuous line represents the distribution of leaf indices amongst thirty-five domestic varieties in common use in Great Britain. See Appendix I. The broken line represents the distribution of leaf indices amongst thirty-five seedlings derived from parents of common domestic types. See Appendix II.

The problem may be attacked from a different angle, viz. the variation of leaf type to be found in the European, the Peruvian and the Chilean material.

In Fig. 1 are shown graphs recording the distribution of the leaf indices of thirty-five common British domestic varieties and thirty-five seedlings of similar origin respectively. The extent of the variation is the same in both, but whilst the mean index of the domestic varieties is 84, that of the seedlings is a somewhat higher one, viz. 93, which suggests that while there may well be a genetic basis controlling the relations represented by the leaf index, there is still a possibility of reaching higher leaf indices by further selective breeding.

A similar conclusion is suggested by the evidence obtained from the curve (Fig. 2) representing a Peruvian *S. andigenum* family derived from a parent form with a leaf index of 53, and its twenty-one natural seedlings, the mean index of the family being 58.

A genetic basis underlying the variant types of leaf in the *S. andigenum* potato series would explain how it has been possible, by selection amongst seedling progeny raised in England, to evolve our distinctive domestic potato type from an apparently unlike ancestral stock.

In Fig. 3 are set out on one graph the leaf indices of the twenty-nine plants from the Chiloean area, whilst the other records the leaf indices of eighty-two seedlings derived from three families of Chiloean parents. Here, as in our English domestic series, Fig. 1, not only is the range of variation between parent forms and their offspring alike, but the distribution of leaf form in both parents and seedlings is remarkably similar. It is to be noted, however, that in the British domestic series (Fig. 1), the range of variation both of parents and seedlings is much narrower than in the Chilean series, a fact which may be interpreted as implying that a more controlled and continuous selection of type has

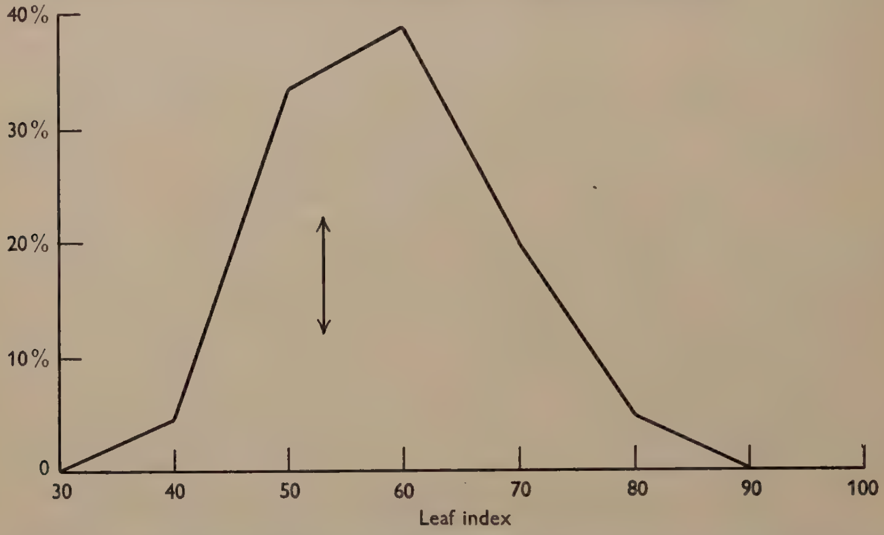

Fig. 2. A curve representing the distribution of leaf indices in a natural selfed family of twenty-one seedlings grown at Corstorphine in 1953 derived from a Peruvian *S. andigenum* parent, leaf index 53, see arrow.

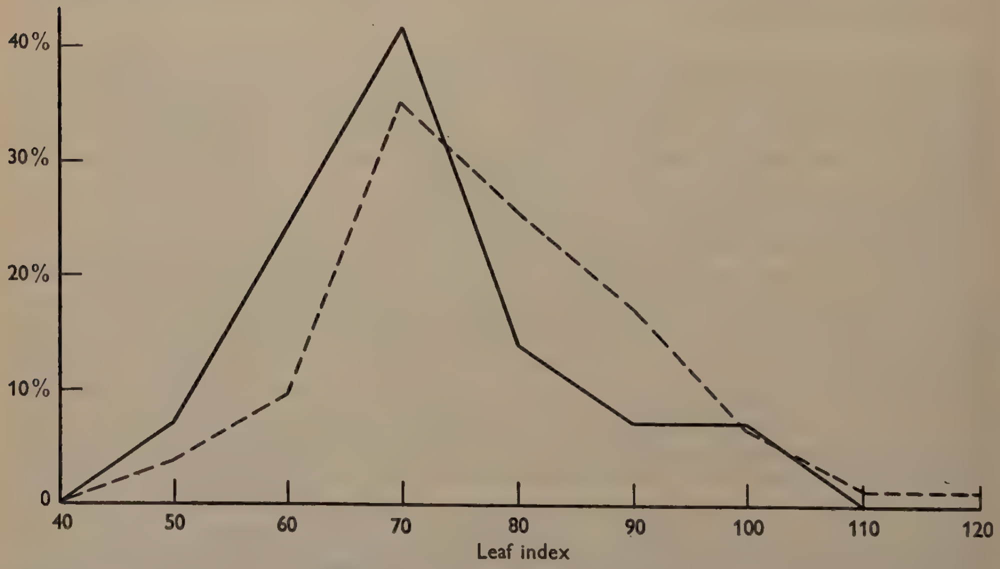

Fig. 3. The continuous line represents the distribution of leaf indices amongst twenty-eight Chilean native varieties, and the broken line represents the distribution of leaf indices amongst eighty-two seedlings derived from parents of native Chilean origin. See Appendix III.

been exercised during the last three centuries in the raising of our varieties than has been exercised in Chile.

Müller reports that the commonest type of domestic potato plant grown in the Chiloe province is known as Corahilla. All Corahilla varieties bear tubers with coral-coloured skins. They throw up sixteen or more slender stems, and bear twenty or more rather small tubers (Fig. 4).

Sixteen Corahilla plants occur amongst the specimens sent to me by Dr Müller; the distribution of whose leaf indices is shown in Fig. 5. In this figure there are set out two graphs: one representing the leaf indices of the sixteen Corahilla varieties, the second curve recording the indices of thirteen non-Corahilla varieties.

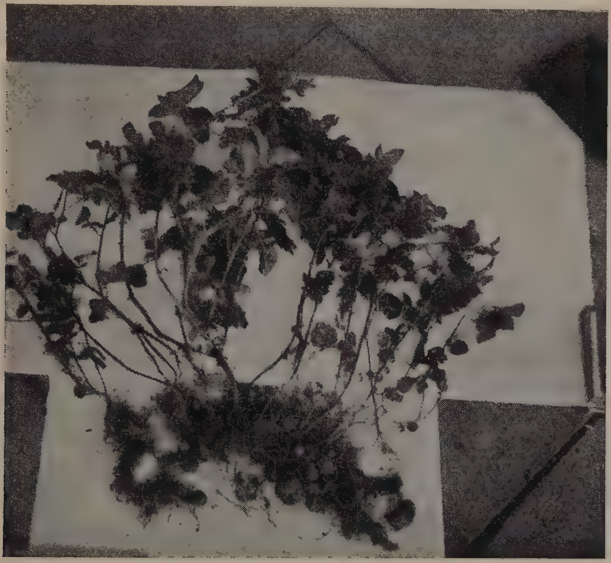

Fig. 4. A Chilean potato plant of the Corahilla variety, planted towards the end of October 1951 in Puerto Octez and raised 19 January 1952. The plant bears twenty tubers on sixteen stems.

The Corahilla group is relatively uniform, half of its numbers showing the same leaf shape, a result which is not unexpected, seeing that the type has been subjected to prolonged selection.

In the non-Corahilla group the variation is greater than in the former, including as it does, a few specimens of outstanding high indices equal to the best of those to be found in the north of South America or in our own domestic varieties.

The conclusion reached may be summed up as follows:

The varieties of potato under review whether emanating from the Chiloe province or from the province of La Serena are, for the most part, straightforward examples of the species *S. andigenum* which we have come to know so well in the north of South America. There would appear to be no reason based on morphology why we should look to Chile rather than the former for the original home of the European potato.

The domestic potato of Europe, though given the specific name of *S. tuberosum* is in fact a variety of the species *S. andigenum* which has acquired its present range of characteristic forms of leaf and habit as a result of prolonged selection for higher cropping varieties on the one hand and early or late maturity on the other. In short, man has created the various domestic types of *S. tuberosum* by planned breeding and selection from the original *S. andigenum* of South America in much the same manner as he has won for his use the widely divergent types of the domestic horse from the shaggy, sturdy pony of paleolithic times.

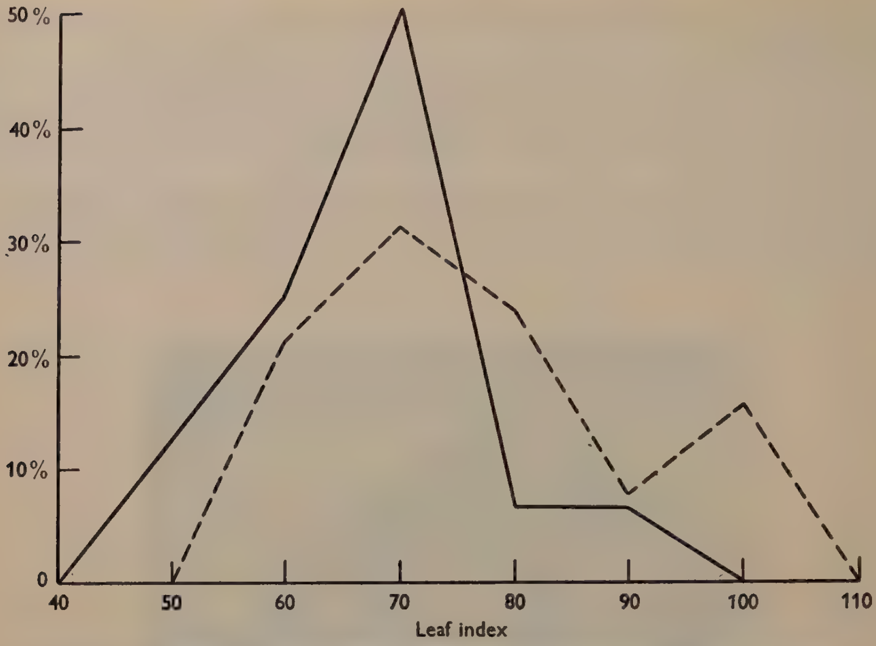

Fig. 5. The continuous line represents the leaf indices of sixteen *Corahilla* plants; the broken line, thirteen other native Chilean varieties.

APPENDIX I

A list of thirty-five domestic varieties and their leaf indices

Variety	Index	Variety	Index
Arran Comrade	84	Lochar	110
Arran Consul	88	Majestic	79
Arran Pilot	76	President	94
Arran Viking	77	Red Fife	68
British Queen	78	Rhoderic Dhu	112
Catriona	86	Sharpe's Express	86
Conference	88	Stormont Dawn	72
Craig's Alliance	83	Sutton's Olympic	88
Craig's Bounty	93	Ulster Chieftain	80
Craig's Royal	92	Ulster Cromlech	83
Craig's Snow-White	67	Ulster Earl	66
Di Vernon	77	Ulster Emblem	68
Doon Star	94	Ulster Ensign	71
Duke of York	88	Ulster Leader	71
Gigantic	83	Ulster Premier	76
Golden Wonder	80	Ulster Supreme	70
Kerr's Pink	100	Up-to-date	71
King Edward	91		

APPENDIX II

Three families of seedlings derived from domestic parents

(1)	Abundance × Flourball	13 seedlings
(2)	Bravo × Flourball	10 seedlings
(3)	May Queen × Flourball	12 seedlings

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The wild fodder Sorghums of the section Eu-Sorghum. By J. D. Snowden, F.L.S., Economic Botanist (Retired), Uganda.

(With 20 Text-figures)

[Read 6 May 1954]

HISTORY AND CLASSIFICATION

Sorghums have been cultivated for their grains or sweet stems since ancient times, but little attention was given to the small-grained wild Sorghums until the beginning of the twentieth century when some of them were introduced into the United States of America, where they soon became popular and were extensively cultivated as fodder for stock. Linnaeus, in the first edition of his *Species Plantarum*, published in 1753, included the Sorghums known to him under the genus *Holcus*, and described the wild race he knew as *H. halepensis*. The same species was referred to by Scopoli (*Flora Carniolica*, ed. 2, **2**, 274, 1772) under *Andropogon arundinaceus*. Later, when the *Holcus* of Linnaeus was divided into several genera, the Sorghums were transferred to the genus *Sorghum* by Moench (in *Methodus Plantas*, p. 207, 1794); and Persoon (in his *Synopsis Plantarum*, **1**, 101, 1805), the latter referring the wild Sorghums to *S. halepense*. Brotero, however (in *Fl. Lusitanica*, **1**, 89, 1804), placed the Sorghums in the genus *Andropogon* and made the combination *A. halepensis* for the wild species. In his Monograph of the Andropogoneae Hackel (in De Candolle's *Monographiae Phanerogamarum*, **6**, 499, 502, 1889) classified all the races of *Sorghum* under *Andropogon sorghum*, placing the cultivated species under the subspecies *sativus* and the wild ones under the subspecies *halepensis*.

It was suggested, by Hackel, in 'Die kultivirten Sorghum-Formen und ihre Abstammung' (in Engl., *Bot. Jahrb.* **7**, 115–26, 1885), and Koernicke (in *Handbuch des Getreidebaues*, **1**, 300, 1885), that the cultivated Sorghums had been derived from varieties of *A. halepensis*. This led some botanists to infer that all the cultivated varieties had been derived from one wild ancestor. Piper, who had studied many of the Sorghums under cultivation in the United States, as well as the herbarium material in that country, at Kew, and in Berlin, in his revision of *A. halepensis* and *A. sorghum* (in *Proc. Biol. Soc. Wash.* **28**, 25–44, 1915) pointed out that Hackel had indicated that they had arisen from those varieties without perennial rootstocks, such as *effusus*, *virgatus*, and *aethiopicus*, and not from those having original rhizomes. Piper then classified the wild races of the former under eleven subspecies of *A. sorghum*, and placed those with rhizomes under six subspecies of *A. halepensis*.

In his revision of the African Sorghums Stapf (in Prain, *Fl. Trop. Afr.* **9**, 104–54, 1917) decided to retain *Sorghum* as a separate genus. He discussed the classifications of Hackel, Koernicke and Piper, pointed out the desirability of recognizing smaller units, and described all the wild and cultivated species of Tropical Africa known to him. He divided them into two sections, namely *Eu-Sorghum*, containing twenty-seven species, where among the wild Sorghums many of Piper's subspecies were given specific rank, and *Sorghastrum*, in which he placed six species of a distinctive group that Nash (in Britton, *Manual of the Flora of the Northern States and Canada*, p. 71, 1901) had described as a new genus under the name of *Sorghastrum*.

In my 'Classification of the Cultivated Sorghums' (in *Kew Bull.* pp. 222, 223, 1935) I decided to keep *Sorghastrum* Nash separate from *Sorghum*, as the plants of this group differ from the true Sorghums, especially in the solitary primary branches of the panicle, which are often much branched quite near the base so that they appear to be falsely semi-verticillate; the pedicelled spikelets usually reduced to the hairy pedicels; and the glabrous lodicules. The lower glume is also usually shorter than the upper. The separation of *Sorghastrum* left a more uniform genus *Sorghum* which was divided into two sections, characterized as follows:

I. *Eu-Sorghum:* sheath-nodes glabrous or finely pubescent, not bearded; primary branches of the panicle divided (at least the lower); racemes lateral and terminal; number of chromosomes (in those species that have been examined) $2n=20$, or $2n=40$.

A. Subsection *Arundinacea*: annuals, or tufted perennials without rhizomes; number of chromosomes usually $2n=20$ (rarely $2n=40$). This subsection is divided into two series, *Spontanea*, containing the wild Sorghums, and *Sativa*, embracing the cultivated Sorghums.

B. Subsection *Halepensia*: perennials possessing distinct elongated rhizomes; number of chromosomes usually $2n=40$; wild Sorghums.

II. *Para-Sorghum*: sheath-nodes bearded (at least the upper); primary branches of the panicle simple; racemes terminal; number of chromosomes $2n=10$; wild Sorghums.

An account of the cytological work carried out by Garber (in *Amer. Nat.*, **78**,89–94, 1944) supports the separation of *Para-Sorghum* as a distinct section and tends to confirm that the Sorghums of this group are unlikely to have been concerned in the evolution of the cultivated Sorghums. Most of the species of this group are slender grasses with little bulk and, as they do not appear to have any special importance as fodder for stock, they are not dealt with further in this account of the Arundinaceous Forage Sorghums.

The wild Sorghums of the two subsections of *Eu-Sorghum* are very similar in most characters, but those of the *Halepensia* group, besides possessing rhizomes and usually having a higher number of chromosomes, generally show little tendency to hybridize with the cultivated grain Sorghums. They also have a different area of distribution, which extends from the Mediterranean region eastwards to India and south-western Asia. On the other hand, the wild Sorghums of the series *Spontanea* and the cultivated races of the series *Sativa*, which belong to the subsection *Arundinacea*, are frequently found to hybridize with one another in regions where Sorghums are grown for their grains and sweet stems, and the wild races of this subsection are mainly distributed in tropical and subtropical Africa.

The relationships of the wild and cultivated Sorghums were reviewed in my account of the 'Grain and Sweet-stemmed Sorghums' (*The Cultivated Races of Sorghum*, pp. 234–40, 1936). A few of the more important intermediate races that appear to have arisen naturally, and not as a direct result of artificial cross-fertilization, are included below, together with the other wild races of the section *Eu-Sorghum*. Although they generally agree with the wild Sorghums in possessing small grains enclosed by the glumes, they have somewhat tougher racemes resembling those of the cultivated races. Those cultivated Sorghums that show signs of degeneration as a result of intercrossing with wild species, generally indicated by the racemes shattering and the spikelets readily falling, will be excluded from this revision. In connexion with the cross-pollination that occurs between the different races of Sorghum, it is of interest to record that in India, in the course of experiments undertaken to procure early-maturing races of sugar cane, by means of artificial cross-fertilization, hybrids between *Sorghum* and *Saccharum* have been raised, thus indicating the possibility of a closer relationship between these two genera than has generally been accepted.

As so many specimens of wild Sorghums have been received at Kew since Dr Stapf's account of the Tropical African species was published in 1917, a revision of those belonging to the section *Eu-Sorghum* has now become practicable and indeed has been found necessary in order to facilitate the identification of the material, especially that received from North-east, Central, and East Africa. In dealing with these Sorghums, however, it should be noted that the descriptions of the species and varieties are based on the dry herbarium specimens, although amplified in some cases by information from collectors' notes.

GENERAL CHARACTERS OF THE WILD SPECIES OF SECTION *EU-SORGHUM*

Annual or perennial grasses one to several metres high. *Culms* slender to stout, usually terete, often woody and reed-like, few to many noded, simple or sometimes branched above, usually glabrous and green but often with purplish markings and a grey waxy bloom. *Leaves* alternate; sheaths usually clasping the culms when young, often shorter than the mature internodes, generally glabrous except for a little pubescence near the base, along the margins and near the junction with the blade; ligule usually a membranous or scarious rim 1–3 mm. long, ciliate from the back; blades convolute in bud but soon becoming flat, usually linear to linear-lanceolate, narrowing upwards to an acuminate tip, glabrous except for a few hairs near the ligule and the junction with the sheath, mostly light to dark green with a paler, often broad and pronounced, mid rib, sometimes with purplish markings, generally spinulously scabrid on the margins, especially upwards.

Panicles usually compound or decompound, varying much in shape and size, generally loose and open on erect peduncles, at length more or less exserted from the uppermost leaf-sheath; rhachis usually continuous, often striate or channelled, with the angles spinulously ciliate, at least upwards; branches 1–6 (rarely more) from a node, usually hairy at the base and also in the angles of the divisions, often scabrid. *Racemes* terminal and lateral on the branchlets, which may arise from near the base, or 1–5 cm. or more from the base, of the branches, 1- to 7-noded (rarely more), mostly fragile and generally readily disarticulating at maturity, but sometimes rather tough; internodes (joints) and pedicels very similar, but the internodes often more dorsally compressed and almost flat on the face, slender to filiform, ciliate along the sides, the pedicels generally with almost discoid or sometimes oval tips; spikelets mostly in pairs composed of one sessile and one pedicelled, except at the end of each raceme where there is usually one sessile and two pedicelled spikelets.

Sessile spikelets dorsally compressed, varying in shape, mostly awned but sometimes awnless, with a small blunt, usually bearded, callus at the base of the lower glume; florets 2, the lower floret usually reduced to its lemma. *Glumes* equal or almost equal in length, usually coriaceous for the most part but thinner towards the tips and with a thin transverse basal strip 0·3–0·5 mm. wide, rarely thinner and subcoriaceous to papery or crustaceous throughout, the margins papery to membranous, narrowly incurved, those of the lower clasping the upper (except when in flower), so that when closed they more or less conform to the shape of the spikelet in outline; lower glume flattened or only slightly convex on the back, mostly 10- to 15-nerved, but usually with only 3–5 nerves outwardly evident near the tip, generally with short cross-nerves scattered in the middle third or three-fifths, the margins narrowly inflexed upwards, 2-keeled from about the middle or in the upper third or fourth, with the scarious spinulously ciliolate keels usually narrowly winged (marginate) and terminating in minute teeth just below the hyaline apex, or sometimes gradually merging imperceptibly with it; upper glume convexly boat-shaped, usually 7-nerved (rarely more), the central nerve finely keeled and scaberulous above the middle or near the tip, short cross-nerves usually present in the middle third or three-fifths, the incurved margins hyaline and usually finely long-ciliate, at least upwards. *Lemmas* hyaline, thinly membranous and often very fragile, the margins incurved and usually finely ciliate; lower lemma (when flattened out, as in the following descriptions) almost similar in shape and size to the lower glume but a little shorter and with the apex obtuse or slightly notched, usually with two fine nerves, one on each side, but sometimes with a third central nerve; upper lemma usually 1–2 mm. shorter than the lower, ovate to ovate-elliptic, finely 1- to 3-nerved, the two lateral often short or obscure, the apex 2-lobed and with an awn from the sinus, or sometimes entire, or almost entire, and then muticous or mucronate; awn usually abruptly bent near the middle, the lower half tightly twisted to form a straight stem or column and glabrous or finely pubescent along the spirals, the upper part or bristle being only slightly twisted and finely scaberulous along the margins. *Palea* like the lemmas in texture, generally a little shorter than the upper lemma, almost linear to linear-lanceolate, nerveless, with the margins finely, and usually sparsely, ciliate. *Lodicules* 2, somewhat wedge-shaped, about 1–2 mm. long, usually ciliate, but the cilia sometimes reduced to a few or one at each corner. *Stamens* 3, anthers linear, usually yellow. *Styles* 2, terminal or subterminal, with the plumose stigmas sometimes purplish and usually laterally exserted for pollination. *Ovary* glabrous. *Grains* (caryopses) elliptic, obovate-elliptic, or obovate, generally not exceeding half the length of the glumes when mature, more or less dorsally compressed, with the hilum face almost flat and the embryo face convex, the embryo-mark oval and usually about half, or rather more than half, the length of the grain.

Pedicelled spikelets mostly linear-lanceolate to subulate, often much narrower than the sessile, but sometimes little different in size, usually awnless, the upper floret ♂ or sometimes reduced to the lemma like the lower; glumes thinner than those of the sessile spikelets, herbaceous to membranous, with the nerves usually plainly visible throughout their length, otherwise much like those of the sessile in shape and nervation; lemmas like those of the sessile in texture, shape, and nervation, but often reduced in size and the upper usually muticous; palea small or often absent; lodicules like those of the sessile spikelets when present, but smaller and often almost glabrous; anthers mostly smaller than those of the sessile spikelets, but similar in shape and colour.

THE POISONOUS PROPERTIES OF SORGHUM

Cases of Sorghum poisoning or cyanogenesis, resulting from the presence of hydrocyanic or prussic acid in plants used for fodder, have been reported from many countries during the last fifty years. The toxicity varies not only in different species but also in the same species, because the amount of acid present differs according to the conditions under which the plants are grown and the particular stage of growth. The poisonous tendencies are generally greatest in the young immature plants, especially in such luscious dark green growths as are apt to follow the application of an excess of nitrogenous manures, heavy rainfall, or irrigation, after a dry spell of weather, and in the stunted growths due to checks caused by drought, frost, or insect and fungous attacks. Generally it is not considered advisable to feed animals on Sorghums until the plants have reached the flowering stage, although sometimes the immature grains may also prove injurious. At maturity, however, most of the Sorghums grown under normal conditions are considered harmless. The danger of poisoning tends to be reduced if the Sorghums are cut and dried before being fed to stock, but drying does not always immediately destroy the toxicity; much depends on the method of drying. The poisonous properties of some of the Sorghums under review will be referred to again under the notes dealing with the utility of the species.

KEY TO THE GROUPS AND SPECIES OF SECTION *EU-SORGHUM*

Subsection **Halepensia**: perennials with well-developed more or less extensively creeping rhizomes; sessile spikelets deciduous when mature, 3·8–6·2 mm. long; grains small, enclosed by the glumes; number of chromosomes usually $2n=40$; wild Sorghums:

Sessile spikelets more or less obtuse, elliptic to subelliptic or elliptic-lanceolate, 4–5·5 mm. long; glumes coriaceous; lower glume with the keels ending in distinct minute teeth, forming with the subhyaline apex a more or less distinct 3-toothed tip:

Leaf-blades narrow, 0·5–2 cm. wide (rarely more); culms slender, 0·5–1·5 m. high, up to 5 mm. wide; panicles small, often somewhat contracted after flowering, up to 25 cm. long and 5 cm. wide, with the lower branches about 5–8 cm. long. 1. *halepensis.*

Leaf-blades somewhat broad, mostly 2–4 cm. wide when mature; culms slender to robust, up to 1 cm. wide, usually 2–3 m. high; panicles large, loose and spreading, generally 25–55 cm. long, 10–25 cm. wide, with the lower branches 10–25 cm. long. 2. *miliaceum.*

Sessile spikelets acute to acuminate; glumes subcoriaceous with somewhat papery tips; lower glume with the keels ending without or with only obscure teeth:

Sessile spikelets 5–6·2 mm. long, acuminate to acute, often awned; panicle small, 15–30 cm. long, lower branches 5–15 cm. long; culms usually 0·5–2 m. high, 0·3–1 cm. wide; leaf-blades narrow, 0·5–2 cm. wide. 3. *controversum.*

Sessile spikelets 3·8–5 mm. long, abruptly acute with a short fine point, usually awnless; panicle large, 20–60 cm. long, lower branches 15–20 cm. long; culms 2–3 m. high, 1–3 cm. wide; leaf-blades broad, often 3–5 cm. wide. 4. *propinquum.*

Subsection **Arundinacea:** annuals, or tufted perennials without rhizomes, the tiller-culms arising from basal buds near the foot of the previous season's culms; number of chromosomes usually $2n = 20$ (rarely $2n = 40$):

Series *Sativa*: racemes tough; mature sessile spikelets persistent; grains large, often exceeding the glumes in size, usually much exposed; Sorghums cultivated for their grains or sweet stems (the species of this series are not dealt with in this revision).

Series *Spontanea*: racemes usually fragile, rarely somewhat tough; mature sessile spikelets usually deciduous, sometimes rather tardily; grains small, enclosed by the glumes; wild Sorghums:

Racemes fragile, readily disarticulating at maturity, the sessile spikelets falling together with the adjoining internode of the rhachis and its pedicelled spikelet, or at least its pedicel:

Sessile spikelets lanceolate, 6–8 mm. long, awns 8–18 mm. long; leaf-blades usually 0·5–2 cm. wide, rarely up to 3 cm.:

Panicle long and narrow, 15–60 cm. long, 1–5 cm. wide, with the branches usually suberect; sessile spikelets 6·5–7 mm. long, 2–2·5 mm. wide, acute, awn slender; grains obovate-elliptic, about 2·5–3 mm. long, 1·5–2 mm. wide. 5. *virgatum.*

Panicle ovate-oblong to lanceolate, 20–40 cm. long, up to 15 (rarely 20) cm. wide, with the branches soon spreading; sessile spikelets 6–8 mm. long, 2–3 mm. wide, shortly acuminate, awn rather stout; grains obovate-elliptic to obovate-oblong, 3–3·5 mm. long, 2–2·5 mm. wide. 6. *lanceolatum.*

Spikelets not as above:

Sessile spikelets 6–9 (rarely 5·5) mm. long:

Sessile spikelets 2·5–3·5 mm. wide, 6–9 mm. long:

Sessile spikelets 8–9 mm. long, elliptic- to oblong-lanceolate, acuminate, awnless, or more often with an awn 8–16 mm. long; panicle large, loose, 15–45 cm. long, 5–25 cm. wide. 7. *vogelianum.*

Sessile spikelets 6–8 mm. long, usually with awns 20–30 mm. long:

Panicle very narrow, 10–40 cm. long, 3–10 cm. wide; branches usually suberect; sessile spikelets elliptic- to ovate-lanceolate, usually densely and persistently tomentose with mostly whitish silky hairs; awn 20–30 mm. long. 8. *aethiopicum.*

Panicle rather wide and loose, up to 35 cm. long, 8–15 cm. wide, branches subflexuous and spreading; sessile spikelets elliptic-lanceolate to elliptic-oblong, shortly and finely, often fulvously, hairy, or at length almost glabrous on the backs of the glumes; awn 20–25 mm. long. 9. *macrochaeta.*

Sessile spikelets 2–2·5 mm. wide, usually 6–7·5 mm. long, but sometimes reduced to 5·5 mm., elliptic- to oblong-lanceolate; grains obovate-elliptic to obovate, 2–3 mm. long, 1·5–2 mm. wide:

Upper lemma of the sessile spikelet awnless or with an awn 5–10 mm. long; sessile spikelets elliptic- to oblong-lanceolate, narrowly acuminate; leaf-blades usually broad, mostly 3–6 cm. wide; panicle large, loose and much branched, 20–60 cm. long, 10–25 cm. wide. **10**. *arundinaceum*.

Upper lemma of the sessile spikelets with an awn 10–16 (sometimes 18) mm. long; leaf-blades narrow, mostly 1–2·5 (but sometimes 3) cm. wide:

Leaf-blades mostly 45–60 cm. long, narrowing upwards to an acuminate tip; sessile spikelets elliptic-lanceolate, acuminate, 6–7 (or sometimes 5·5) mm. long; panicle pyramidal to elliptic-oblong, at length loose and spreading, 15–50 cm. long, 5–15 cm. wide, lower branches up to 15 cm. long. **11**. *verticilliflorum*.

Leaf-blades up to 30 cm. long; panicle narrow-oblong, 1–2 cm. wide:

Leaf-blades 10–30 cm. long, with a long-tapering filiform tip; sessile spikelets elliptic-lanceolate to elliptic, acute, 5·5–6 mm. long; awn 16–18 mm. long; panicle 10–25 cm. long. **12**. *somaliense*.

Leaf-blades 4–10 cm. long, acuminate; sessile spikelets oblong-lanceolate, acuminate, 5·5–6·5 mm. long; awn 12–14 mm. long; panicle 4–12 cm. long. **13**. *pugionifolium*.

Sessile spikelets 4–5·5 mm. long, 1·5–2·5 mm. wide:

Upper lemma of the sessile spikelet with an awn 10–16 mm. long:

Leaf-blades broad, usually 3–5 (but sometimes 2) cm. wide when mature; panicle wide and loose, 15–50 cm. long, 10–30 cm. wide:

Sessile spikelets elliptic-ovate, acute to acuminate, 4·5–5·5 mm. long, 2–2·5 mm. wide. **14**. *brevicarinatum*.

Sessile spikelets elliptic-lanceolate to elliptic-oblong, obtuse or subacute, 4·5–5·2 mm. long, 1·5–2 mm. wide. **15**. *usambarense*.

Leaf-blades narrow, 1·5–2·7 cm. wide; panicle narrow and loose, up to 40 cm. long and 10–15 cm. wide; sessile spikelets broadly elliptic to elliptic-oblong, obtuse, 4–4·5 mm. long, 2–2·5 mm. wide. **16**. *castaneum*.

Upper lemma of the sessile spikelets with a small mucro; sessile spikelets elliptic to elliptic-oblong, subacute, 4–5 mm. long, 1·5–2 mm. wide; panicle narrow, loose or somewhat contracted, 20–25 cm. long, about 6 cm. wide; leaf-blades (uppermost) 1·5–2 cm. wide. **17**. *panicoides*.

Racemes more or less tough or tardily disarticulating; sessile spikelets persistent or at length deciduous:

Panicle dense and contracted with the rhachis often completely hidden by the branches, 10–20 cm. long, 3–8 cm. wide; leaf-blades broad, 4–8 cm. wide; sessile spikelets ovate to broadly elliptic-ovate, acute to acuminate, 6–7·5 mm. long, 2·5–3·5 mm. wide. **18**. *hewisonii*.

Panicle loose, with the rhachis more or less freely exposed when mature; leaf-blades narrow, 1–3 cm. wide:

Sessile spikelets 6–7·5 mm. long, 2–3 mm. wide, elliptic to elliptic- or oblong-lanceolate, subacute; pedicelled spikelets persistent; grains elliptic to obovate-elliptic, 3·5–4·5 mm. long, 1·5–2 mm. wide. **19**. *sudanense*.

Sessile spikelets 4·5–6 mm. long, ovate, ovate-lanceolate, or elliptic-ovate to elliptic-rotund; pedicelled spikelets deciduous:

Sessile spikelets ovate to ovate-lanceolate, 4·5–5·5 mm. long, 2–2·5 mm. wide, acute to acuminate; grains broad-elliptic to obovate-elliptic, 2–2·5 mm. long, 1·5–1·8 mm. wide; panicle sublinear, about 18 cm. long and 2 cm. wide. **20**. *elliotii*.

Sessile spikelets elliptic-ovate to elliptic-rotund, 4·5–6 mm. long, 2–3 mm. wide, acute to acuminate and closed, or subacute and slightly open at the tip; grains obovate-elliptic to obovate, 3–4 mm. long, 1·5–2·5 mm. wide; panicle oblong to elliptic-oblong, 15–40 cm. long, 8–15 cm. wide. **21**. *niloticum*.

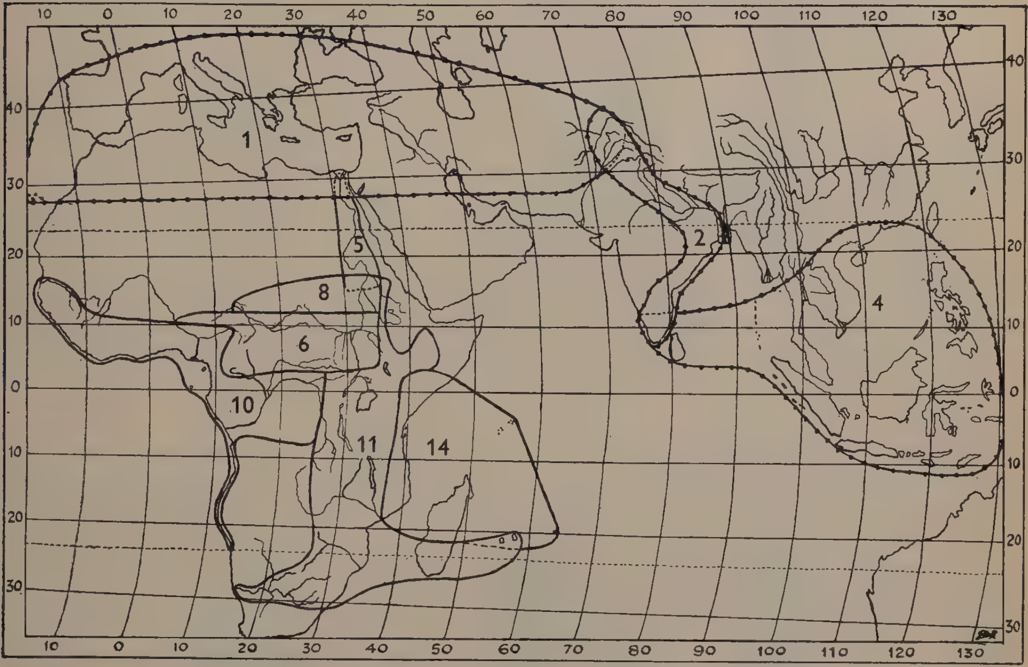
DESCRIPTION AND ENUMERATION

Subsection **Halepensia** Snowden in *Kew Bull.* p. 222, 1935

1. **Sorghum halepense** (Linn.) Pers.

Holcus halepensis Linn., *Sp. Pl.* ed. 1, p. 1047, 1753. When he described this species Linnaeus did not cite any specimens in support of it, but there are two specimens in his herbarium at The Linnean Society of London, and one of them which I have examined is written up *halepensis* in his own handwriting. Linnaeus gives the habitat of his species as Syria and Mauritania.

Andropogon arundinaceus Scop., *Fl. Carn.* ed. 2, **2**, 274, 1772, was the name used for a specimen from Carniola, but Scopoli cites earlier synonyms of Linnaeus and his species is evidently based on *Holcus halepensis* Linn.



Distribution of the chief species: 1, *Sorghum halepense*; 2, *S. miliaceum*; 4, *S. propinquum*; 5, *S. virgatum*; 6, *S. lanceolatum*; 8, *S. aethiopicum*; 10, *S. arundinaceum*; 11, *S. verticilliflorum*; 14, *S. brevicarinatum.*

Milium halepensis (Linn.) Cav., *Descr. Pl.* p. 306, 1802, is founded on *Holcus halepensis* Linn.

Blumenbachia halepensis (Linn.) Koel., *Descr. Gram.* p. 29, 1802, is based on *Holcus halepensis* Linn. His new genus was not generally accepted by other botanists.

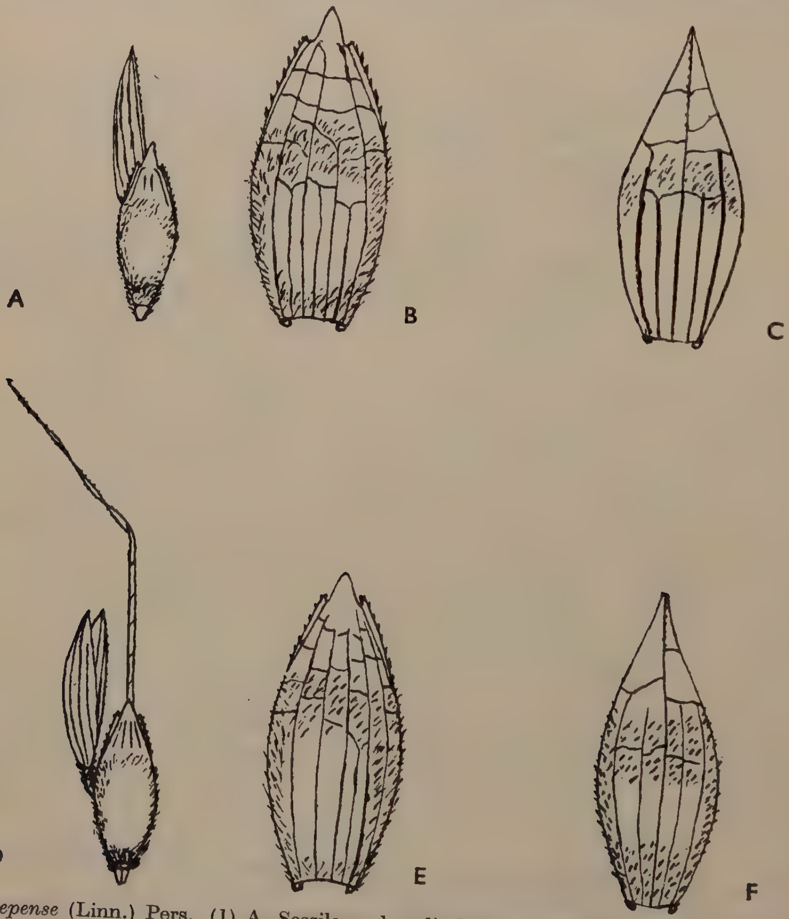
Andropogon halepensis (Linn.) Brot., *Fl. Lusit.* **1**, 89, 1804, rests on *Holcus halepensis* Linn.

Sorghum halepense (Linn.) Pers., *Synops.* **1**, 101, 1805, is based on *Holcus halepensis* Linn.

Andropogon sorghum (Linn.) Brot. subsp. *halepensis* (Linn.) Hack. var. *halepensis* Hack. in *DC. Monogr. Phan.* **6**, 502, 1889, is founded on *Holcus halepensis* Linn., but besides reducing *halepensis* to a subspecies Hackel also includes some elements in his var. *halepensis*, which in my opinion do not belong to *Holcus halepensis* Linn. Some of the species cited by Hackel in synonymy are therefore excluded, particularly *Andropogon* *laxus* Roxb., *Fl. Ind.* **1**, 271, 1820, *A. controversus* Steud., *Synops.* **1**, 391, 1854, and *Sorghum giganteum* Edgew., *J. As. Soc. Bengal*, **21**, 181, 1853, as well as all the varieties of Hackel's subsp. *halepensis* other than var. *halepensis* (sensu stricto).

DESCRIPTION

A perennial with abundant creeping rhizomes 25–75 cm. long, often descending to a depth of 25–50 cm. *Culms* rather slender, mostly simple but sometimes branched, 0·5–1·5 m. high, up to 5 mm. wide near the base. *Leaves* usually 7–10; blades linear, narrowed to a point at the apex, 20–60 cm. long, 0·5–2 (rarely 2·5) cm. wide, the stoutish midrib pale green to almost white and contrasting with the darker green of the remainder. *Panicle* loose when in flower, somewhat contracted after flowering, lanceolate to lanceolate-oblong, mostly 10–25 cm. long, and 3–8 cm. wide; branches slender, suberect, one to several from each node, the lower usually about half the length of the panicle, bare of spikelets for 1–5 cm. from the base. *Racemes* fragile, 1- to 5-noded, up to 2 cm. long; internodes and pedicels slender, 2·5–4 mm. long, rather densely ciliate with whitish to tawny or purplish hairs 0·7–1 mm. long. *Sessile spikelets* elliptic to subelliptic, mostly



Sorghum halepense (Linn.) Pers. (1) A, Sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view (awnless form, from *Snowden*, Kew, 1933). (2) D, sessile and pedicelled spikelets; E, lower glume; F, upper glume (awned form; from *Haradjean* 3470). A and D, ×5; B, C, E and F, ×10.

4·5–5 mm. long, but sometimes up to 5·5 mm., 1·8–2·3 mm. wide, obtuse or subacute, at first more or less hairy and cream to buff-yellow or tawny, with 3–4 nerves evident near the tip of the lower glume, at length often purplish to blackish brown or black and sometimes almost glabrous; awned or awnless; callus-beard copious to somewhat scanty. *Glumes* firmly coriaceous with slightly thinner tips; lower usually 7- to 9-nerved, with a few cross-nerves above the middle, keeled in the upper fourth, the wings of the keels widening upwards to end in minute teeth, forming with the short apex a distinctly 3-toothed tip, spinulously scabrid on the keels; upper 7-nerved, with a few cross-nerves from the middle upwards, rough on the keel in the upper third. *Lemmas* moderately and finely ciliate; lower elliptic to elliptic-oblong, 4–5 mm. long; upper ovate to ovate-elliptic, 3–3·5 mm. long, 1- to 3-nerved, acute and minutely mucronate, or 2-lobed to about 0·5 mm. deep and with an awn 10–16 mm. long. *Anthers* 2·5–3 mm. long. *Grains* light to dark brown, oblong-obovate, 2·5–3 mm. long. *Pedicelled spikelets* at length deciduous, often purplish, ♂ or sometimes neuter, 4·5–6 mm. long; lower glume 7- to 9-nerved, upper 5- to 7-nerved; anthers 2·5–3 mm. long.

Diagnostic characters and affinities

The distinguishing features of *Sorghum halepense* are the abundance of the slender wide-spreading rhizomes, the rather slender dwarf culms, narrow leaf-blades 20–60 cm. long, 0·5–2 (rarely 2·5) cm. wide; small panicles that are usually somewhat contracted after flowering; and the elliptic to subelliptic sessile spikelets, 4·5–5 or sometimes 5·5 mm. long, 1·8–2·3 mm. wide, with the tip of the lower glume obtuse or subacute and distinctly 3-toothed. It is closely related to *S. miliaceum* (Roxb.) Snowden, but the latter has taller culms, larger wide-spreading panicles, and somewhat more elliptic-lanceolate sessile spikelets, as well as shorter thicker rhizomes closely knitted to form dense mats.

Distribution and utility

S. halepense is distributed throughout the Mediterranean Region, where it is most frequent in the islands and coastal lands of the countries bordering the Mediterranean Sea. It also occurs in many inland districts where the soil and climatic conditions are favourable. It is usually found in or near cultivated lands and pastures, but it is also met with on untilled lands, in waste places and by roadsides. Many specimens are recorded as having been collected in, or near the borders of, vineyards, and it would appear that *S. halepense* thrives under similar conditions to those which have been found to be most suitable for Grape Vine cultivation.

The occurrence of *S. halepense* in some areas adjacent to the Mediterranean Sea, such as Portugal, the Canary Islands and Madeira Islands, may be part of its natural distribution or due to some early introduction from Spain and North-west Africa. Eastwards of the Mediterranean its distribution extends across Asia Minor and the Levant to Iran, Turkmen, Afghanistan, Western Pakistan and Kashmir, although in the drier districts of some of these territories it is generally confined to irrigated or cultivated lands. After examining all the Sorghum material available at Kew I am of the opinion that *S. halepense* is not indigenous to any part of India as at present constituted, but is replaced somewhere in the neighbourhood of the North-West Frontier Province of Pakistan and Kashmir by the closely related *S. miliaceum*, which has a more south-easterly distribution and succeeds better in a warmer climate. *S. halepense*, however, must have been introduced into the Punjab and United Provinces of India at some early period, and is now found in most provinces of India, in some cases having been used for the purpose of experimental cultivation and trial as a fodder crop for domestic animals.

During the last hundred and twenty years. *S. halepense* has been introduced into most countries throughout the world where suitable warm-temperate or subtropical conditions prevail. In some of them, such as those of Central and Western Europe, including southern England (where it is not usually grown for feeding to stock), it is not common, but is sometimes found as an alien on rubbish tips, and waste lands, or occasionally it is cultivated in Botanic Gardens. In countries where the winters are severe, it is rarely able to establish itself under natural conditions, although it may persist in sheltered gardens for many years. On the other hand, in many territories where it has been introduced and cultivated as fodder for stock, it has found conditions so favourable that it has become a noxious weed, difficult to eradicate because of the vigour and abundance of its wide-spreading rhizomes.

It is of interest to note, however, that *S. halepense* has not extended from North Africa southwards into Tropical Africa, nor has it established itself to any great extent in other tropical countries. This may be partly due to the fact that fodder crops are not generally grown for feeding livestock in the tropics and little attention has been paid to its cultivation, but it seems more probable that this species requires a longer growing period to mature than most tropical African Sorghums, as well as a distinct resting-period brought about by cold weather during a comparatively wet season which keeps the rhizomes reasonably moist, in contrast to the conditions prevailing in most tropical countries, where the resting stage usually occurs during the hot dry season when the land is usually baked hard with the sun and the old vegetation often subject to destructive fires.

Attention to the importance of *S. halepense* as a fodder plant was largely due to its successful cultivation in many parts of the United States in the first half of the nineteenth century. According to Piper (in *Proc. Biol. Soc. Wash.* **28**, 27, 1915) it was first introduced from Turkey in 1830. Since then it has been widely cultivated (under the name of Johnson Grass) in many States, especially those south of latitude 36°, where in some districts it has become naturalized. From the United States it has spread to Mexico and many countries of Central and South America, as well as the islands of the Carribean Sea. It has also been grown on a large scale in South Africa and in some States of Australia, especially Queensland, where it has also become naturalized in some areas. During later years its cultivation as fodder has declined to some extent, partly because of the difficulty of eradicating its rhizomes from cultivated lands, and also because of the more recent introduction of *S. sudanense* (Piper) Stapf, commonly known as Sudan Grass, which has been found to provide equally good feed for stock as well as having the advantage of being more easily controlled because of the absence of rhizomes, which is characteristic of the Sorghums of the subsection *Arundinacea*, to which it belongs. Hybrid strains between Sorghums of this latter subsection and *S. halepense* have now been successfully obtained under cultivation in South America. As these are said to have less troublesome rootstocks than the true species it is possible that some of these new varieties may help to restore *S. halepense* to its former good favour. Specimens of these hybrids that I have seen at Kew show close relationship with cultivated Sorghums of the subseries *Drummondii*.

Since the beginning of the present century the poisonous properties of *Sorghum halepense* have received much attention from scientists, and the results of their investigations have been published in various scientific and agricultural journals, including those of the United States of America, South Africa and Australia. Useful data concerning some of these experiments have been brought together in *The Poison Plants of New South Wales*, by Evelyn Hurst, published in 1942. In Montana, United States, the plants were found to be dangerous when growth was stunted, and especially noxious when rank growth was produced in irrigated soils. In Queensland, Australia (according to White, in *Qd Agric. J.* 1934), the plants are least harmful when in full seed. The danger is minimized if the plants are cut and allowed to wilt before being fed to stock. Dealing with Sorghums in the United States in 1935, Ball considered that Johnson Grass contained a greater percentage of HCN than any other cultivated Sorghum. According to the New South Wales Department of Agriculture, the underground parts, which are white and succulent, are said to have caused losses in both cattle and pigs. The results of other experiments show that positive results of hydrocyanic acid have been obtained both from the older leafy portions and from young leafy shoots. On the other hand, in an experiment where 3 lb. of freshly cut plants, consisting of old shoots, mainly with heads well matured, were fed to sheep of 103 lb. weight, negative results were obtained. It was also found that drying does not immediately destroy the toxicity of Johnson Grass, as lucerne hay containing 75 % of Sorghum caused the loss of twenty-eight head of cattle in an hour, although the hay had been cut 2 days previously and the sun had been hot during that period. In this latter experiment the cattle were very hungry when fed. Strong positive reactions for HCN were obtained both from the hay and the ingesta of the dead animals. The above examples will be sufficient to indicate some of the dangers that may result from using this Sorghum as fodder for stock, especially in the case of freshly cut and immature plants, although in countries where stock have been accustomed to feed on it no harm results under normal conditions, and it provides the animals with good nourishing food.

Forms and varieties

Since *S. halepense* was first recognized as a distinct species, a number of forms or varieties have been described by various authors. A frequent variation of the spikelets is the presence or absence of an awn to the upper lemma. The majority of the plants have awned spikelets, but sometimes in specimens of the same gathering and number the spikelets of one panicle are awned and those of another awnless, and it is not uncommon to find most of the spikelets in a panicle awnless but accompanied by a few that are distinctly awned. The awned form has generally been accepted as typical of the species, and Hackel (in *DC. Monogr. Phan.* **6**, 502, 1889) describes it under *Andropogon sorghum* (Linn.) Brot., subsp. *halepensis* (Linn.) var. *halepensis* subvar. *genuinus* Hack. It is referred to by Stapf (in Hook. *Fl. Brit. Ind.* **7**, 182, 1896) under *A. halepensis* (Linn.) Brot., var. *genuinus* Hack (under which he also includes *Andropogon miliaceus* Roxb.); and by Acherson and Graebner (in *Synops. Mitteleur. Fl.* **2**, Pt. I, 47, 1898) under *A. halepensis* (Linn.) Brot. var. *typicus*.

The awnless state was described by Hackel, loc. cit., as *A. sorghum* (Linn.) Brot., subsp. *halepensis* (Linn.) var. *halepensis* subvar. *muticus* Hack., and it has also received the following names: *A. halepensis* (Linn.) Brot. var. *muticus* (Hack.) Aschers. & Graebn. (loc. cit.); *A. halepensis* (Linn.) Brot. subsp. *anatherus* Piper (in *Proc. Biol. Soc. Wash.* **28**, 28, 1915); and *Sorghum halepense* (Linn.) Pers. f. *muticum* (Hack.) C. E. Hubbard (in Hook., *Ic. Pl.* **34**, 1938, under t. 3364, p. 4).

A glabrous form of the awned state was described by Hackel, loc. cit., as *Andropogon sorghum* (Linn.) Brot. subsp. *halepensis* (Linn.) var. *halepensis* subvar. *leiostachys*. In addition, Hackel, loc. cit., refers to a broad-leaved form, *Sorghum halepense* (Linn.) var. *latifolium* Willk. & Lange (*Prodr. Fl. Hisp.* **1**, 48, 1861), which is described as 5 ft. high, with leaves ¾–1 in. wide, and a panicle a foot or more long. Although I have seen two of Willkomm's specimens from Spain, neither of them is from the type locality, nor do they agree with the above description. On the other hand, this name and description might well be applied to some of the robust forms, found in Europe and other regions, that have evidently been grown under most favourable conditions and are probably either cultivated plants or grown in or near to cultivated lands.

In contrast to these robust forms there are dwarf specimens with slender culms about 50 cm. high, leaves 0·5–1 cm. wide, and small panicles, that evidently represent impoverished plants grown under adverse conditions, such as infertile soils and low rainfall, or may have resulted from close grazing by stock or frequent cutting for hay. Often such specimens have well-developed rhizomes, and under favourable conditions would have grown into average-sized plants. There are also slender-culmed forms that appear to have matured under shady conditions that have led to elongation and weakness of the culms with looser longer-branched panicles than usual. When grown in the open the lower branches of the panicle are generally comparatively short except, as sometimes happens, where only one or two of the lowermost whorl develop, because the panicle fails to emerge properly from, or is too tightly held by, the uppermost leaf-sheath. In such cases the remaining branch or two tend to be longer than usual and should be disregarded when reckoning the average length of the panicle branches. The size of the spikelets, also, may differ to some extent according to the robustness of the plants, but they also vary somewhat in shape and size with the stage of development. They are generally longest at the flowering period or immediately after flowering, tending to become a little shorter and narrower as they become more plump and rounded with the increasing size of the grains.

As most of the above forms and variations appear to be mainly due to the influence of climate and habitat, and careful examination of the material at Kew has failed to reveal reliable characters suitable for dividing the species into distinct varieties, I have thought it best to leave these variable forms to be investigated in the field, by growing them under similar conditions, in order to determine if any of them are worthy of varietal status. In the enumeration of the specimens given below, however, the awned state is denoted by an * immediately after the name or number of the collector. A few more notable variations are mentioned in the text.

ENGLAND. Southern counties: Fishponds, Bristol, *Sandwith* *! Brighton, Sussex, *Smart* *! Kew, Surrey, *Snowden*! Middlesex, *Welch* *! Dagenham, Essex, *Lousley**! *Melville* *! Wanstead, *Nash* *!

FRANCE. Mostly in southern districts: Banks of the Loire River, *Perret* *! Avignon, *Hort. Bot. Divionensis* *! *Delacour* *! *Requiem*! Tarascon, *Gay*!

CORSICA. Etang de Biguglia, *Mabille* 66! 66 *! Corté district, *Kralik, Pl. Corses* *!

SPAIN. Motril, Granada province, *Willkomm, iter Hispanicum* 286! Chiva, near Valencia, *Willkomm, iter Hispanicum* 528 *! Near Murcia, *Bourgeau, Pl. d'Espagne* 1533 *!

BALEARIC ISLANDS. From sea-level up to 1220 m. Minorca: Fornells (Sept. 1935), *Kennedy* 86 *! Majorca: Pollensa and Aleudia (July, 1936), *Kennedy* 86! 253 *!

PORTUGAL. Near Lumiar, *Welwitsch, Pl. Lusitanicae, Inlio* *!

SWITZERLAND. At the Rhone dam, near Sion, *Kneucher, Gram. Exsicc.* 182!

HUNGARY. Aleppoi Czirok, *Degen in Gram. Hungarica* 101 *!

ITALY. Lombardia district, *Petri Portae* (July 1865) *! (Oct. 1867) *! Near Riva, on Lake Garda, *Kneucher, Gram. Exsicc.* 63 *! Parma, *Gay* (Aug. 1826) *! Near Naples, *Alexander* (1845)! (July 1845) *!

SICILY. Near Pelizzi, Nebrodi mountains, *Flora Nebrodensis, Strobly* (Aug. 1873) *! Palermo, *Todaro, Fl. Sieuta Exsicc.* 496! 496 *!

TRIESTE. Without precise locality: *Prihoda* (Oct. 1864) *! *Tidoll* *!

YUGOSLAVIA. Istria, Zaule, *Schultz herb. normale Englehardt* 2599 *! Near Fiume (Rijeka), *Smith* (July 1869) *! Constantza near Mangalia, *Cretzoiu* (July 1827) *! Isaccea, in Tulcea district, *Cretzoiu* (July 1837) *! Lesina Island, Dalmatia, *Bottori* *!

The specimen from Istria, *Schultz* 2599, is a robust form that may have been grown on cultivated lands.

ALBANIA. Between Durazzo (Durres) and Berat, *Alston & Sandwith* 2516!

This is a robust specimen with the panicle in fruit.

RUMANIA. Without precise locality, *Trivaldski* (1837) *!

BULGARIA. Hills north of Varna, *Gilliat-Smith* 984 *!

GREECE. Macedonia, at Kopriva and south of Karamudli, *Turrill* 368 *! 490! 490 *! Thrace, at Xanthi, *Tedd* 444 *! Attica, *Heldreich, Pl. exsicc. de Graecia* *! Drakofto, Pelloponnesus, *Davis* 1012! Without precise locality, in Graecia (Berger) *Mus. Monach* (1837) *!

CEPHALONIA. Without precise locality, in vineyards, *Schimper & Wiest* (1834) *!

CRETE. Canea province: Kissamos and Platania, *Elisée Reverchon, Pl. de Crete* (1883 & 1884) 183 *! *Gandoger, Herb. Creticum* 7359 *!

Turkey (in Europe). Thrace: Gallipoli, Suala, and Anzac, *Ingoldby* 595! 595 *! *Kett* 90 *!

Turkey (in Asia). Antalya, 30 m. *Tengwall* 31 *! Ain-Halakim, Mount Nusairy, 760–900 m., *Haradjian* 3470 *! Near Ermenck, Plains of Cilicia, *Cosson* 213 *! Near Mardin, Kurdistania, *Sintensis* 1341 *! Schiherè sur, Kurdistania, *Hausknecht* (1867)! Karadagh, *Fischer*!

Cyprus. Kythraeae, *Sintensis* 679 *! Timben and Limassol, 15 m., *Syngrassides* 389! 717 *! Kyrenia, at sea-level, and Platres, 1130 m., *Kennedy* 82! 83 *! 84 *! Near Perapedhi, 1067 m., *Davis* 1851 *! Larnaca, *Ussher* 124 *! Nicosia, *Lindberg* *! Without precise locality, often causing poisoning to animals, *Rae* *!

Syria. Northern Syria, Aintab, 610 m., *Haussknecht, Syriaco-Armeniacum* (1865) *! Southern Syria, El Hutch, *Lowe* (1863–4) *! Without precise locality, *Gandoger* (1920) *! *Kneucker Gram. Exsicc.* 63*a* *! *Blanche* 56 *!

Palestine. Amaltha, *Hayne* (Oct. 1872) *! Ghor-es-Safieh, *Hart* (1883–4) *! Wad el Kelt, Khan Yubb Yusif to Ain el Tabigha, sea-level to 100 m., ex *American Colony, Jerusalem* B 6066 *! B 66 *! Northern Circle, poisonous to grazing animals (except horses, mules and donkeys), *Agric. & Forests Dep.* (*Mason*) 4 *! Jerusalem, *Forest Dep.* (*Gabrielith*) 48 *! 48!

Tunisia. Near Zaghouan, *Kralik* 310 *!

Algeria. Oran province, Sidi-bel-Abbès, *Warion* 2286 *! Alger province, Blidah, *Lefebre* 186! Stora, *Bòvé* (Aug. 1889)!

Morocco. Southern Morocco, Mzuda, *Hooker* (May 1871) *!

Canary Islands. Gran Canaria, Beo de Angustura, ex *Herb. Monig. Murray* *! Without precise locality, presented Hooker, Feb. 1868, *Gay*!

Madeira Islands. Near Gorgulho, ex *Herb. Monig. Murray* *! *Mandon* 262! Near Funchal, *Clarke* 94 *! *Grabham* 31! *Lowe* 26! Dos Saltos, *Hooper* (Jan. 1842) *! Without precise locality, *Lawrence* (July 1837) *! *Leman*! *Lowe*! Masson *!

Belgian Congo. Introduced as a fodder plant, Eala, *Lebrun* 604!

Southern Rhodesia. Introduced for trial as a fodder plant, Agricultural Experiment Station, Salisbury, *Mundy* 50*b*, *Trapnell* 754 *! Insiza, 1370 m., *Capstick* 2328 *! Lomagundi district, 1070 m., *Eyles* 3149 *!

Portuguese East Africa. Zambesi Delta, Boruma, *Meynharth* 1046 *!

South Africa. Transvaal: Pretoria, Froenkloof Experiment Farm, and without precise locality, *Nat. Herb. Pretoria* H. 20939 *! 8498 *! (Waterval No. 7) 1544 *! Natal: in Botanic Gardens, not indigenous, *Medley Wood* 6675!

Medley Wood's specimen has a loose panicle and looks as though the plant had been grown in a shady habitat.

Iraq. Northern district, *Imperial Institute* I! Remount Farm, Karredah, *Graham* *! West Baghdad, *Rogers* 0303! Rustam Experimental Farm, Baghdad, *Lozer* 3416 *! *Guest* 184! 275 *! 2459 *! Aziziyah, *Guest* 3567! Zauritch, 915 m., *Guest* 3750! Basra, *Haussknecht, Syriaco-Armeniacum* (1865)!

Iran. Near Teheran, *Trott* 863 *!

Turkmen (Turcoman). Kizil Arvat, Karakala, *Sintensis* 1890!

Afghanistan. Without precise locality, *Griffith* 356 *! 661 *! 6825!

Pakistan. Baluchistan: Bolan Pass (ex Herb. Leman, 1852) *Griffith* *! Chitral, 1500 m., *Harris* *! Drosh, 1370 m., *Toppin* 307 *! Without precise locality, *Wingate* *! Gilgit: Hunza Valley, 1675 m., *Duthie* 12318 *!

Kashmir. Shadipur—Jhelum Valley, *Ludlow & Sherriff* 7803! Without precise locality, near towns, *Jacquemont* (388) 656 *! *Herb. Falconer* *!

India. Punjab: West of Chenab River, *Hooker & Thomson* (Nov. 1846) *! Plains below Mumior, *Hooker & Thomson* *! Bhyrowal, 45 miles east of Lahore, *Hooker & Thomson* (Sept. 1846) 1542! Timoo Ghat, *Hooker & Thomson* (Oct. 1846)! Without precise locality, *Hooker & Thomson* *! Jellundur, *Wingate* (Sept. 1888) *! In valley below Nahan Sirmur, *Jacquemont* (144) 2518! United Provinces: near Mustafabad, *Hooker & Thomson* (Oct. 1846)! Bengal: Botanic Gardens, Calcutta, *Narayanaswami* (April, 1918) *! Serampore, *Griffith* *! Madras: Samalkota, Godaveri district; Betta Mogilam, Hosur, and Metigiri, Salem district, *Madras Herb. S. India Flora* (June 1917) *! (Dec. 1913)! (Dec. 1916)! 15451 *! Shencottah to Aryankavu, Travancore State, *Calder & Ramaswami* 669 *! Province and locality uncertain, *Wight Herbarium* 1673 *!

Robust specimens from plants used for hybridization experiments with *Saccharum*, *Janaki Ammal* 1236, which have persistent spikelets, are probably hybrid forms of *Sorghum halepense*. A specimen from the Botanic Gardens, Calcutta, *Nashe* 1317, which also has persistent spikelets, may have resulted from intercrossing between *S. halepense* and a cultivated Sorghum.

CEYLON. Peradeniya Herbarium (seeds from Drieberg) *Galston* 2240!

JAVA. Without precise locality, *Posthumus* 89!

A poor specimen from Java, raised from seeds introduced from Valparaiso, *Brigsman* (Mar. 1914), may belong to *S. halepense*, but the material is too scanty for exact determination.

FORMOSA. Kontay Experiment Station, near Koshun, from a sample of Johnson Grass hay, *Price* (June 1912) *!

AUSTRALIA. Western Australia: Bassendean, *Palmer* *! Bayswater, near Perth, *Stoward* 234! Williambury, Minilya River, *Bunbury* *! Queensland: near Brisbane, *Bailey* (Dec. 1913) *! *Blake* 318 *! Burpengary, *Blake* 136 *! Cloncurry, *Blake* 201! Near Brisbane; Moreton district; between Grandchester and Laidley; near Mt. Gravat; between Laidley and Forest Hill; and between Teirotville and Anthony, *Hubbard* 3026! 4316 *! 4732 *! 5285 *! 5352 *! 5388! 8075 *! 8906 *! Forest Hill, *White* 5 *! Johnson River, *Harding* (Nov. 1907) *! Kigaroy, *Jensen* *! Atate Farm, Hermitage, Warwick, *Liverseed* 8 *! Riversleigh Eidsvold Line, *Turner*! Christmas Creek, *McIntyre Bros.* 7! New South Wales: Ashfield, *Cheel*! Without precise locality, *Brisbane Botanic Gardens Herbarium* 9 *! Victoria: Without precise locality, *National Herbarium, Melbourne*!

NEW ZEALAND. Napier, naturalized, *Kirk* 1387 *!

FIJI ISLANDS. Introduced experimentally to feed stock but now a troublesome weed, without precise locality, *Greenwood* 392!

Greenwood's specimen has rhizomes and leaves typical of *Sorghum halepense* but it has no inflorescence.

HAWAII. Nuwanu Valley, Oahu, *Forbes*!

UNITED STATES. California: Redding, Shasta county, *Smith* 744 *! Santa Cruz county, *Woolley-Dod* 453! Mesa Grande, 760 m., San Diego county, *Spencer* 1393 *! Oklahoma: Harmon county, *Stevens* 1087! Texas: San Antonio, Bexar county, 185 m., *Heller* 1706 *! Without precise locality, ex United States National Herbarium, *Walley* (1886) *! Arkansas: Van Buren Bluffs, Crawford county, *Demaree* 3167! Louisiana: Without precise locality, *Ball* 80! Tennessee: Near Nashville, *Curtiss* 3644 A! Virginia: Norfolk, *Hitchcock* 277! South Carolina: near Columbia, *Curtiss* 3644 *! Florida: Indian River, Merritt Island, *Curtiss* 5724! Hillsborough county, *Fredholm* 6346! Miami and Buena Vista, Dade county, *Moldenke* 522! 704 *!

Only a few spikelets of Moldenke's 704 are awned.

MEXICO. Sonora: Guamas, *Palmer* 64! Coahuila: Saltillo, 1600 m., *Arsène* 3464 *! Nuevo Leon: near Monterrey, 540 m., *Abbon* *! *Arsène* 498 *! Michoacan: Zitacuara to Las Anonas and to San Jose Purua, 1575–1775 m., *Hinton* 13140 *! 13270! 13270 *! Guerrero: Pungarabato, Coyuca, *Hinton* 5457! Mexico: Temaxcaltepec district, 1750 m., *Hinton* 4031! 1427! 1427 *! Yucatan: Izamal, Gaumer 720!

The specimen *Hinton* 4031 has the appearance of having been grown in a shady habitat.

Bermuda Islands. Paget, and Trott's Pond, *Brown & Britton* 130! 135!

Cuba. Near Havana, *Curtiss* 561 *!

Porto Rico. Finca, Bueno Causejo, Rio Piedras, *Hioraw* *!

Santo Domingo. Cibas Valley, Santiago province, *Ekman*!

Jamaica. Blue Mountains district: St Andrew and Resource, *Perkins* 1479 *! 1139 *! Resource, 1100 m., *Harris* 11521! 1000 m., *Harris* 11582 *! Richmond Park, St Andrew, *Harris* 12706! Hope Grounds, 215 m., *Harris* *! Without precise locality, *Botanic Department, Jamaica* 2004 *!

The unnumbered specimen of *Harris*, from Hope Grounds, has only a few spikelets with awns.

St Lucia. Near Government Experiment Station, Union, *Box* 323!

Costa Rica. Las Concavas, *Lankester* 210 *!

Venezuela. Cetu, Caracas and La Guayra, 610–915 m., *Fendler*, *Plantae Venezuelanae*, 1854–55, 1653! Caracas, 915 m., *Munro*, *Plantae Venezuelanae*, *July* 1858, 2629! Cumana, *Füncke* 245!

British Guiana. Botanic Gardens, Georgetown, *Actson* 115 *!

This specimen is a shady habitat form.

Paraguay. Cordillera de Altos, *Hassler*, *Plantae Paraguarienses*, 3346 *!

Argentina. Villa Sujan, 460 m., Tucuman province, *Venturi* 313 *! Near Cnel. Roca, 250–360 m., *Fischer* 216! Near Santa Fé, Santa Fé province, *Job* 1067 *!

Uruguay. Soriano, Mercedes district, *Berro* 6387 *!

2. **Sorghum miliaceum** (Roxb.) Snowden

Andropogon miliaceus Roxb., *Fl. Indica*, **1**, 276, 1820, is based on specimens grown at Calcutta from seeds collected in the mountains north of Oude, which were sent from Lucknow under the name of Hill Grass. There are no authentic specimens of Roxburgh's plant at present known to me, but the drawing of it, no. 1717 in Icones Roxburghianae[1], illustrates the large size and loose branching of the panicle, and the dissections of the sessile spikelets show them to be short and wide with the apex obtuse, as stated in Roxburgh's description. Two enlarged drawings of the sessile spikelets are given. In one of them the upper lemma has a short awn less than twice the length of the lemma, but in the other it is awnless. The glumes are shown as shortly hairy and the lemmas as shortly ciliate. Roxburgh states that the leaves are ensiform-lanceolate, 2–3 ft. long and 1–2 in. wide near the base where they are broadest.

Andropogon miliformis Schultes, *Mantissa*, **2**, 448, 1824, is a change of name for *A. miliaceus* Roxb. This change of name was made by Schultes because the name *A. miliaceum* had appeared (without description or author) in Brouss., *Cat. Monsp.* p. 5, 1804, among several other species of *Andropogon*, also without descriptions or authors except for *A. aculeatum* Forsk., which appeared near the bottom of page 4.

Roemer et Schultes, *Syst. Veg.* **2**, 828, 1817, refer in a note to four species of *Andropogon*, which are insufficiently known to them, thus:

Quid: *Andropogon foveolatus* Descript de l'Egypt, t. 8?
A. aculeatus Forsk. apud Brouss., *Cat. Monsp.* 1804.
A. miliaceus Forsk. apud Brouss., *Cat. Monsp.* 1804.
A. radiatus P. de Beauv.

There is nothing in Brouss., *Cat. Monsp.* 1804 to connect Forskal with *A. miliaceum*, and it seems possible that Schultes may have been mistaken in assuming that because it appeared immediately below *A. aculeatus* Forsk. in Roemer et Schultes, loc. cit., *A. miliaceus* was also one of Forskal's species. Kunth, *Enum. Pl.* **1**, 507, 1833, and Dietrich, *Synops. Pl.* **1**, 410, 1839, refer to *A. miliformis* Schultes as a synonym of

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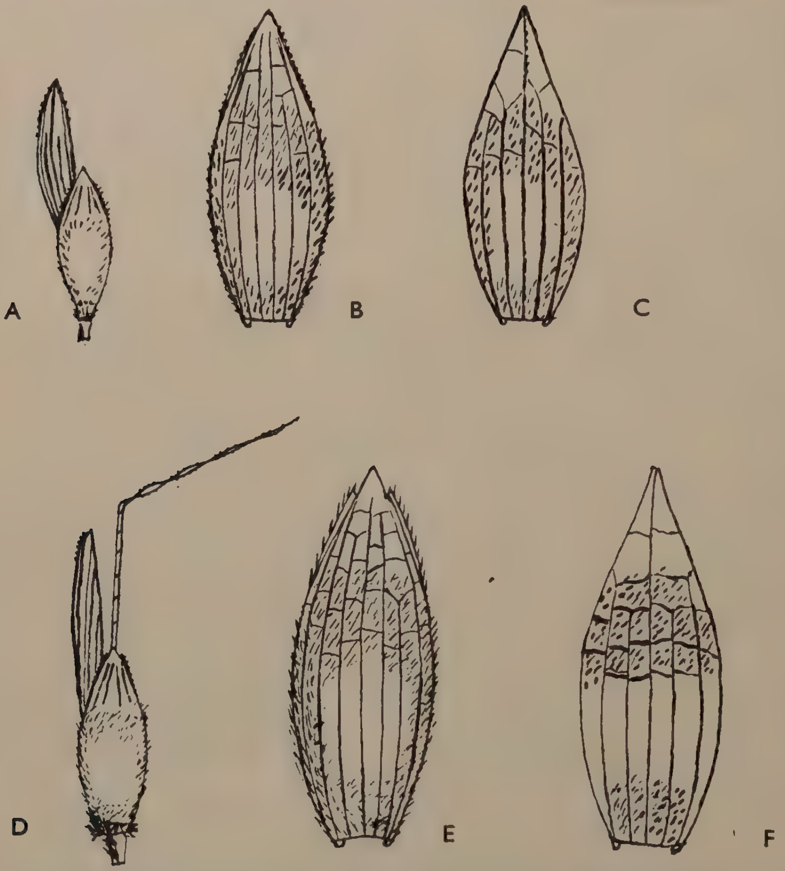
[1] These Icones consist of a few sets of unpublished drawings of Roxburgh's plants, one set of which I have seen at Kew.

A. miliaceus Roxb., and Steudel, *Nomencl. Bot.* ed. 2, **1**, 92, 1840, refers to the latter as *A. miliaceus*, Brouss., Forsk., Aegyptus? Hackel, in *DC.*, *Monogr. Phan.* **6**, 1889, makes no reference to *A. miliaceus* Forsk., but (loc. cit., p. 541) places *A. miliformis* Schultes in synonymy under *A. miliaceus* Roxb.

In Roxburgh's *Hortus Bengalensis*, p. 1814, *A. miliaceus* is stated as having been received from General Martin, from Hurdwar (probably north of Delhi). As General Claude Martin died on 13 September 1800, the seeds must have been sent to Roxburgh, who came to the Calcutta Gardens in 1793, between the latter date and 1800. As Roxburgh was exchanging seeds, etc., with Sir Joseph Banks, and Broussonet mentions receiving seeds from Sir Joseph, it is quite possible that the *A. miliaceum* mentioned by Broussonet was that of Roxburgh, and had been raised from seeds sent to Sir Joseph Banks by Roxburgh and passed on to Broussonet. After considering all the available evidence, I have come to the conclusion that there was only one *A. miliaceus*, namely the one described by Roxburgh in *Fl. Indica*, **1**, 276, 1820.



(1) *Sorghum propinquum* (Kunth) Hitchc. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view (from *Loher* 1807). (2) *S. miliaceum* (Roxb.) Snowden var. *miliaceum*. D, sessile and pedicelled spikelets; E, lower glume; F, upper glume, exterior view (from Snowden, Kew, Sept. 1933). A and D, × 5; B, C, E and F, × 10.

Sorghum giganteum Edgew., *J. As. Soc. Bengal*, **21**, 181, 1853, was described in an account of the plants growing in the Banda district, Allahabad division, of the United Provinces, India. Both from the description and from the locality, it is evident that this species is the same as the one Roxburgh had previously described as *Andropogon milia-*

ceus. The type specimen of Edgeworth's species has not been located, but in his herbarium at Oxford there is a specimen, no. 361, 'Keirat Rangal', which agrees with the above description and may be part of the same gathering.

Sorghum miliaceum (Roxb.) Snowden, comb.nov., based on *Andropogon miliaceus* Roxb., *Fl. Indica*, 1, 276, 1820, for the reasons already mentioned above, is here proposed as the correct name for this group.

There are three specimens in the Wallich Herbarium at Kew, nos. 8778 A, B and C, that belong to this species and agree well with the illustration no. 1717 in Icones Roxburghianae, especially if the panicles had been spread out in a more natural manner when mounted. Of these I select no. 8778 B to be linked with the above drawing of Roxburgh's plant, as a typical specimen, to be used until a more authentic type has been located.

Description

A tall loosely tufted perennial with short thick somewhat densely matted rhizomes. *Culms* slender to rather stout, 2–3 m. or more high, 0·5–1 cm. wide near the base, simple or branched above. *Leaves* about 10–12; blades ensiform-lanceolate to linear, from a rather broad base, gradually attenuated upwards to the pointed apex, 30–90 cm. long, 1–4 cm. wide, more or less smooth except for the serrate-ciliate margins, the midrib paler than the remainder and somewhat prominent below. *Panicle* large, loose and spreading, ovate-elliptic, ovate-lanceolate, or pyramidal, mostly 25–55 cm. long, and 10–25 cm. wide; branches subverticillate, slender and flexuous with the tips often drooping, lower often 4- to 5-nate, 10–20 cm. long, often naked for 2–5 cm. from the junction with the main axis. *Racemes* fragile, 2- to 5-noded, 10–22 mm. long; internodes and pedicels slender, 2–4 mm. long, densely ciliate with whitish to fulvous or tawny hairs 0·5–1 mm. long. *Sessile spikelets* elliptic-lanceolate to subelliptic, more or less obtuse, 4–5·5 mm. long, 1·5–2·3 mm. wide, straw yellow to deep cream with 3–5 greenish nerves showing near the tip of the lower glume when young, at length tawny to mahogany red or almost black, sparingly strigose, especially near the base, sides and above the middle; awned or awnless; callus densely to moderately bearded. *Glumes* coriaceous, but somewhat thinner towards the tips; lower 8- to 12-nerved, with a few cross nerves above the middle, keeled in the upper third, with the keel-wings spinulously ciliolate and ending in minute teeth below the hyaline apex to form a 3-toothed tip; upper 7-nerved, the two adjoining the median nerve often rather short, with a few cross nerves in the upper half, scabrid on the keel in the upper third. *Lemmas* moderately to sparingly ciliate; lower elliptic-oblong to elliptic-lanceolate, 3·5–5 mm. long; upper ovate to ovate-elliptic, 2·5–4 mm. long, 2-lobed to 0·5–1 mm. deep and with an awn 10–16 mm. long, or sometimes subentire and mucronate. *Anthers* 2·5–3·5 mm. long. *Grains* obovate-elliptic to obovate-oblong 2–2·5 mm. long, 1–1·5 mm. wide, yellowish brown to dark purplish brown; embryo-mark obscure. *Pedicelled spikelets* usually ♂, 5–6·5 mm. long, at length deciduous, often purplish; glumes herbaceous, lower 7- to 8-nerved, upper 5- to 7-nerved; lemmas well developed; anthers 2·5–3·5 mm. long.

Diagnostic characters and affinities

The distinguishing features of *Sorghum miliaceum* are the thick rhizomes; tall culms 2–3 m. or more high; leaf-blades 1–4 cm. wide; large loose panicles, mostly 25–55 cm. long, 10–25 cm. wide; sessile spikelets elliptic-lanceolate to subelliptic, more or less obtuse, 4–5·5 mm. long, 1·5–2·3 mm. wide, awned or awnless; and the coriaceous glumes, with the lower more or less distinctly 3-toothed at the tip. It is closely related to *S. halepense* but differs from it in the thicker rhizomes, taller culms, wider leaf-blades, larger panicles, and the sessile spikelets usually tending more towards elliptic-lanceolate in outline. From *S. controversum* it differs in the comparatively broader and more obtuse sessile spikelets, the more coriaceous and less hairy glumes, with the lower more distinctly 3-toothed at the tip, and the broader leaf-blades up to 4 cm. wide.

DISTRIBUTION AND UTILITY

The natural distribution of *S. miliaceum* extends from Kashmir and the North-West Frontier Province of Pakistan, across northern India, including the Punjab, United Provinces, Central Provinces, and Bengal, southwards to Madras Province. Its taller and more robust culms indicate that it is more of a jungle grass than *S. halepense*, and this is confirmed by it having been found growing in forests, probably in clearings or near the outskirts. Little information is available as to its cultivation and its introduction into other countries, but it has been grown experimentally in the United States, and also at Kew. It may also have reached Mexico, either from the United States or direct from India as some Mexican specimens, referred to below, are remarkably like the typical *S. miliaceum* of India.

According to Piper (who refers to it under *Andropogon halepensis miliformis* Schultes, in *Proc. Biol. Soc. Wash.* **28**, 29, 1915) seed collected by Hartless at Saharanpur, in the United Provinces of India, was introduced into the United States and cultivated at Arlington Farm, Virginia, where the plants grew to a much larger size than those of typical *Sorghum halepense*, and differed conspicuously in the larger looser panicles, besides having very abundant short thick rootstocks in a dense tangled mass. In the Royal Botanic Gardens, Kew, where in 1933 I collected specimens of a *Sorghum* which proved to be *S. miliaceum*, from plants that were growing near to some clumps of *S. halepense*, similar differences were also noticeable, as well as the broader leaves, 3–5 cm. wide. Unfortunately all the plants of *S. miliaceum* at Kew have since died, apparently being unable to survive the English winters, although those of *S. halepense* have persisted for more than twenty years.

As *S. miliaceum* has not generally been recognized as distinct from *S. halepense*, there is little information available regarding either its utility or its toxic properties. Although its stouter culms and wider leaves would provide plenty of good fodder, it might not be so easy to handle with machinery. The plants would also seem to require a warmer climate than those of *S. halepense*, and their thick rootstocks might be just as difficult to eradicate as those of the latter species. On the other hand, *S. miliaceum* is likely to prove more suitable than *S. halepense* for cultivation under tropical conditions in countries where there is no cold winter season.

(i) Var. **miliaceum**

Var. **miliaceum** is the typical variety founded on *Andropogon miliaceus* Roxb. (*Fl. Indica*, **1**, 276, 1820) and *Sorghum giganteum* Edgew. (*J. As. Soc. Bengal*, **21**, 181, 1853). As the type specimens of the above species have not yet been located, I have selected *Wallich* 8778B, in the Wallich Herbarium at Kew, linked with Icones Roxburghianae Fig. no. 1717, to be used in their place until they are found.

Sessile spikelets 4·8–5·5 mm. long, 1·8–2·3 mm. wide, usually awned; panicle with the lower branches usually 1- to 4-nate, stoutish and stiff below after flowering, slender and flexuous upwards.

ENGLAND. Growing in herbaceous grounds, Royal Botanic Gardens, Kew, Sept. 1933, *Snowden*!

PAKISTAN. North-West Frontier Province: Hazara, Hilkoti, Saran Range, *Inayat* (Sept. 1898) presented *Duthie*! Hazara, Kagan Valley, *Inayat* (Aug. 1896; Herb. Bot. Dep. N. India 20294*a*) presented *Duthie*! Gilgit, *Winterbottom* 976!

KASHMIR. Sunajar, 1615 m., *Gammie*! In Kashmir valley, 1676 m., ?*Clarke* 14805 A!

INDIA. Punjab: Karnal—Ghogripur, *Drummond* 21,089! 21,090! Umritsur, *Clarke* 22,226 A! 22,226 B! Chumba, 1524 m., and 914 m., *Clarke* 23,519! 24,308 A! Himalayas, *Barogh*, 1524 m., *Rich* 908! United Provinces: Mahannddee below Muldah, *Hooker & Thomson* (May, 1850)! Saharanpur, *Gov. Botanic Gardens* (Sept. 1884)! Kampti Falls near Mussoorie, 1067 m., *Stewart*! Province and locality uncertain, *Wallich* 8778 B! Central Provinces: Chanda forests, along streams, *Haines* 5318! Allapalli, *Haines* 3647! Bihar and Orissa: Baudh State, near Tikerapara, *Mooney* 634! Madras: Rampa county, beyond Erragonda, Godaveri district, *Narangaswami* 542! Nilgiris, S.E. Wignaad, Gudalur, 914 m., *Gamble* 15,422! Khoondas, near water, *Hohenacker* 1284! Hill Grove, *Bourne Herbarium*! Begur, Malabar, Wyanaad, 762 m., *Fischer* 4511! Nungambakam, *Herb. Madras. Myson*!

ASSAM. Without precise locality, *Fielding*!

Several of the above specimens, including those of *Clarke*, *Mooney*, and *Fielding*, are weak or shady-habitat specimens. *Hohenacker* 1284, from Khoondas in the Nilgiris, matches the specimen from plants grown in the Royal Botanic Gardens, Kew.

Andropogon halepensis subsp. *miliformis* (Schult.) Piper (in *Proc. Biol. Soc. Wash.* **28**, 28, 1915), in so far as it is based on *A. miliaceus* Roxb., comes under this variety. The species *A. laxus* Roxb. and *A. controversus* Steud., cited in synonymy by Piper, are here excluded, however, and will be described below under *Sorghum controversum*. In his description of *Andropogon halepensis* subsp. *miliformis* Piper gives the width of the leaves as 5–15 mm., whereas in the material I have examined at Kew the leaves of *Sorghum miliaceum* are often 3–4 cm. wide. I have been able to accept only four of the specimens in Kew Herbarium cited by Piper as belonging to *S. miliaceum*, the others I think are better placed under *S. halepense*. I have not seen any of the specimens of the plants referred to by Piper as having been grown in the United States and none of the specimens from that country that I have examined at Kew belongs to *S. miliaceum*. It seems possible that the plants mentioned by Piper failed to establish themselves in the United States, but died out like those grown in the Royal Botanic Gardens, Kew.

The following specimens from Mexico, however, which have tall culms, broad leaves, and large panicles, agree well with *Sorghum miliaceum*. It is possible that they may be the progeny of some of the plants grown in the United States, or from seed introduced direct from India, but it is difficult to account for their appearance in Mexico and, until further information is available, they are somewhat doubtfully placed here:

MEXICO. Sonora: north-eastern Sonora, Colonia Morelos, 800 m., *Santos* 1879! Chihuahua: Guasaremos, Rio Mayo, *Scott Gentry* 2375! Nuevo Leon: Fundicion, near Monterrey, *Arsène* 708! Guerrero: Coyuca, *Hinton* 5552!

(ii) Var. **parvispicula** Snowden

Var. **parvispicula** Snowden, var.nov. Spiculae sessiles 4–4·5 mm. longae, 1·5–1·8 mm. latae, plerumque muticae; panicula nutans rami inferiores 5–7-nati, in totum graciles et flexibiles.

Sessile spikelets 4–4·5 mm. long, 1·5–1·8 mm. wide, usually awnless. Panicle nodding, lower branches 5- to 7-nate, slender and flexuous throughout.

The type of this variety is a specimen in Kew Herbarium, *Gamble* 27,139, collected at Dehra Dun, United Provinces, India.

PAKISTAN. Western Himalaya: Baru, *Duthie*! West Punjab: Rawalpindi, *Aitchison* 116!

INDIA. East Punjab: without precise locality (near Karnal?) *Drummond* 21,088! United Provinces: Dehra Dun, 670 m., *Gamble* 27,139! Dehra Dun, in new forest, 670 m., *Umrao Singh* 383! Province and locality uncertain, *Wallich* 8778 A! 8778 C! Madras: Syadapet (Saidapet), Government Farm (Nov. 1885) *Gamble Herbarium*! Nilgiris, Burliar, 914 m., *Gamble* 14,380! Coimbatore, 1310 m., *Raju & Nagathan* 4927! Salem, Hosur Cattle Farm, 914 m., *Narangaswami* 3061 D! Kudirai Madai, 990 m., *Narangaswami* 3944 D! Biligirirangano, N. Coimbalai–Mysore, *Alagranathan*! Dindigul, 914 m., *Wallich* 8778 D (2)!

The panicle of *Wallich* 8778 D (2) is rather weak and depauperate.

3. **Sorghum controversum** (Steud.) Snowden

Andropogon laxus Roxb., *Fl. Indica*, **1**, 275, 1820, was the name originally given to this species, but it was changed by Steudel because of the earlier *A. laxus* Willd. It was described from plants growing in north-east India that were locally known by the names *Kalamoocha* (Beng.) and *Gaddi-janoo* (Teling.). The figure no. 894 in Icones Roxburghianae shows its loose spreading panicle, and gives dissections of the sessile spikelets.

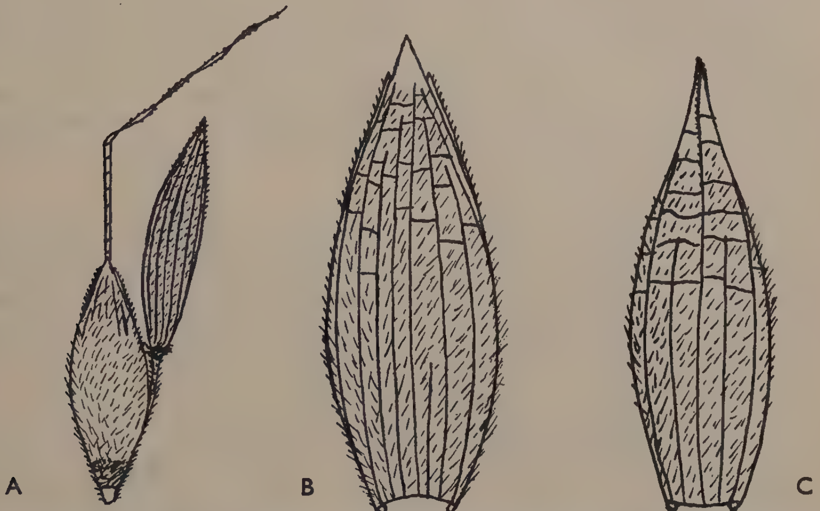
A. controversus Steud., *Syn. Pl. Glum.* **1**, 391, 1854, is based on *A. laxus* Roxb., loc. cit., the change of name being necessary on account of the older *A. laxus* Willd., *Sp. Pl.* **4**, 907, 1806.

Sorghum controversum (Steud.) Snowden, comb.nov., is a change that is necessary on transferring this species to the genus *Sorghum*.

No authentic type specimen of *Andropogon laxus* Roxb. has been located, but in the Wallich Herbarium at Kew there is one sheet written up *A. laxum* and marked H.B., which suggests that the two specimens mounted on the sheet may have been grown in Hort. Bot. Calcutta, from seed of the plants from which the illustration in Icones Roxburghianae was drawn. The right-hand panicle of this sheet certainly agrees well with the illustration, but it differs in having the sessile spikelets awnless. Awned and awnless states belonging to the same species, however, are common in certain species of the subsection *Halepensia*, and these Wallich specimens agree with awnless states of *Sorghum controversum* that have been received at Kew from south-east India. The right-hand panicle of *Wallich* 8778 H has therefore been selected as typical of the awnless state of this species, to be linked with figure no. 894 in Icones Roxburghianae. Until Roxburgh's type specimen has been located, a specimen in Kew Herbarium, *Bourne* 3270, from Tapeswarani, Godavery district, Madras province, dated December 1907, has been selected as characteristic of the awned state of this species.

Description

A more or less loosely tufted perennial, with the rhizomes often somewhat woody. *Culms* erect or sometimes decumbent near the base and rooting at the lower nodes, slender to stoutish and tending to become woody, 0·3–1 cm. wide, 0·5–2 m. high, or sometimes (according to Roxburgh) under favourable moist shady conditions, such as river banks, etc., attaining a height of 3–4·5 m. *Leaves* few to many; blades linear, from a rounded and slightly contracted base, gradually narrowing upwards to the acuminate apex, 12–35 or sometimes 60 cm. long, mostly 0·5–2 cm. wide, more or less smooth except for the scabrous margins. *Panicle* ovate to pyramidal, loose and spreading, often nodding, 15–30 cm. long, 5–15 cm. wide; branches subverticillate, widely spaced, slender and flexuous, except near the base, woolly near the junction with the main axis and in the axils of the divisions, the lower usually 3- to 4-nate, 5–16 cm. long, often naked for 1–5 cm. from the base. *Racemes* fragile, 2- to 5-noded, 8–22 mm. long; internodes and pedicels slender, 2–4 mm. long, densely ciliate with whitish to tawny or pale purplish hairs 0·7–1 mm. long. *Sessile spikelets* elliptic-lanceolate to subelliptic, acute to acuminate, 5–6·2 mm. long, 1·5–2·2 mm. wide, pale straw to cream colour with 3–5 nerves evident near the tip of the lower glume when young, at length tawny to purplish, usually more or less densely softly hairy throughout; awned or sometimes awnless; callus short and narrow, densely bearded. *Glumes* rather thin and subcoriaceous with somewhat papery tips; lower usually 9- to 11-nerved, finely keeled from about the middle or in the upper third, with the narrow keel-margins ending in minute teeth or sometimes merging almost imperceptibly into the hyaline apex, finely spinulously ciliolate on the keels; upper 7-nerved, with two or sometimes four of the lateral nerves often rather short, slightly scabrid on the keel in the upper third or fourth. *Lemmas* densely but finely long-ciliate; lower elliptic-lanceolate to elliptic-oblong, 4–4·5 mm. long; upper ovate to elliptic-ovate, 3–4 mm. long, 2-lobed to 0·7 or 1 mm. deep, with an awn 10–14 mm. long or sometimes with a mucro 1–3 mm. long. *Anthers* 3–3·5 mm. long. *Grains* (immature?) obovate-elliptic, 2–2·5 mm. long, 1–1·3 mm. wide, tan to reddish brown. *Pedicelled spikelets* linear-lanceolate to subulate, usually ♂, 4·5–7 mm. long, 1–1·5 mm. wide, straw yellow or more often purplish, sparsely shortly hairy; glumes thin and papery, lower 7- to 9-nerved, upper 5- to 7-nerved; lemmas large, well developed; anthers 2–3·5 mm. long.



Sorghum controversum (Steud.) Snowden. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume of sessile spikelet, exterior view. A, × 5; B and C, × 10. (From *Bourne* 3270.)

Diagnostic characters and affinities

The most distinctive features of this species are the somewhat woody rhizomes; slender to rather stout and woody culms, sometimes rooting at the lower nodes, short in dry but tall in moist situations; narrow leaf-blades, mostly 0·5–2 cm. wide; loose rather thin panicles 15–30 cm. long, 5–15 cm. wide; the elliptic-lanceolate to subelliptic, acute to acuminate sessile spikelets 5–6·2 mm. long, 1·5–2·2 mm. wide, more or less densely hairy, often with awns 10–14 mm. long; and the rather thin subcoriaceous glumes, the lower one very finely keeled and narrowly margined, the keels without or with only obscure minute teeth. *Sorghum controversum* differs from *S. halepense* and *S. miliaceum* in the more acuminate tip of the usually densely hairy sessile spikelets, the thinner subcoriaceous glumes, the lower one entire or obscurely and very minutely toothed near the apex, and from *S. propinquum* in the more slender culms, narrower leaves and larger, often awned, sessile spikelets.

Distribution and utility

This species is apparently confined to eastern and southern India, extending from Bengal province southwards through Bihar and Orissa to Madras province. Its utility is probably comparable with that of *S. halepense* as regards size and foliage, but little information is available at present as to its usefulness under cultivation, as hitherto it has probably been treated as a form or variety of that species. *S. controversum* seems to succeed best under moist shady conditions, and when growing on moist river banks it often sends out adventitious roots at the lower nodes. In dry soils or when subject to drought, it tends to become dwarf and stunted. It would appear to require a tropical climate in order to succeed.

In the specimens enumerated below those with awned sessile spikelets are distinguished by an * immediately after the name or number of the collector.

INDIA. Bengal: Botanic Gardens, Calcutta, *Wallich Herbarium* 8778 H! Monghyr, *Mokim* 1417! Bihar and Orissa: without precise locality, *Haines* 706 *! S 706 *! Karlapat and Lanigarh, Kalahandi State, *Mooney* 1189 *! 1736 *! Madras: Tapeswarani, Godaveri district, *Bourne* 3270 *! *Gamble* 15,780 *! at 1067 m., *Shevaroy*! Bellary district, *Brougham* *! Travancore, Countalbum, *Ramon Rao* 2111! Coimbatore, Imperial Dep. Agric. India, *Janaki Ammal* 1205 *! Ayinigira Delta, Geddesol, 1371 m., *Cherian Jacob* 356 *! Ramandrug and South Arcot district, *Madras Herb. S. India* 14,383 *! 17,860 *!

Several of the above specimens are damaged by '*Smut Disease*'. In such cases the sessile spikelets are usually awnless. They include *Mokim* 1417 and *Shevaroy*. A specimen from Bombay Reversing Station, Hull Ghat, 460 m., *Wroughton* 34, damaged by the same disease, may also belong to this species.

Hackel (in *DC., Monogr. Phan.*, **6**, 502, 1889) cited *Andropogon laxus* Roxb. (*Fl. Indica*, **1**, 275, 1820) and *A. controversus* Steud. (*Synops. Pl. Glum.* **1**, 391, 1854) in synonomy under *A. sorghum* (Linn.) var. *halepensis* (Linn.); and Piper (in *Proc. Biol. Soc. Wash.* **28**, 28, 1915) cited them in synonomy under *A. halepensis* (Linn.) *miliformis*. I think, however, that although this group belongs to the subsection *Halepensia* it is best kept as a separate species as originally described by Roxburgh.

4. **Sorghum propinquum** (Kunth) Hitchc.

Andropogon affinis J. S. Presl, in C. B. Presl, *Rel. Haenk.* **1**, 343, 1830, is the earliest name known for this species, which was described from specimens collected by Haenke in Luzon, one of the Philippine Islands.

A. propinquus Kunth, *Rev. Gram.* **1**, Suppl. 40, 1830, and *Enum.* **1**, 502, 1833, is based on *A. affinis* J. S. Presl, but the specific name was changed because it was invalidated by the older *A. affinis* R. Br., *Prod. Nov. Holl.* **1**, 201, 1810.

Sorghum propinquum (Kunth) Hitchc. in *Lingnan Sci. J.* **7**, 249, June 1929, is based on *Andropogon affinis* J. S. Presl.

Although I have not been able to see any of the specimens collected by Haenke, I have examined much material from the Philippine Islands, including *Loher* 1806 and 1807 from Luzon Island, as well as other specimens in Kew Herbarium identified by Piper as belonging to this species.

DESCRIPTION

A tall perennial, loosely tufted, with a few stoutish rhizomes often 15–30 cm. long and 3–4 mm. wide. *Culms* mostly 2–3 (rarely 5) m. high, 1–3 cm. wide near the base, sometimes branched above. *Leaves* 15–26; blades linear, from a broad somewhat clasping base, tapering upwards to the acuminate tip, 0·3–1 m. long, mostly 3–5 cm. wide, with the stoutish mid rib prominent below. *Panicles* large, loose, oblong to elliptic-oblong, 5–10 (rarely 15) cm. wide, 20–60 cm. long; branches slender, suberect or slightly spreading above, 1–4 from each node, the lower often 15–20 cm. long and exceeding half the length of the panicle, usually bare of spikelets for 1–5 cm. from the base. *Racemes* slender, fragile, crowded, 1- to 5-noded, mostly 1–2 cm. long; internodes and pedicels slender, 2·5–4 mm. long, sparsely to moderately ciliate with whitish to fulvous hairs about 0·5 mm. long. *Sessile spikelets* elliptic-lanceolate or narrowly elliptic, abruptly acute with a short fine point, 3·8–5 mm. long, 1·2–2 mm. wide, narrowed below to about 0·5–0·8 mm. near the callus; sparsely strigose with whitish to fulvous hairs at the base, sides, and above the middle, straw-yellow to cream-colour with 3–4 delicate nerves visible between the keels of the lower glume when young, at length becoming tawny to mahogany red, blackish brown, or black; usually awnless; callus moderately to sparsely bearded. *Glumes* subcoriaceous to thinly crustaceous in the lower half, somewhat membranous above; lower usually 9- to 11-nerved, finely keeled in the upper third, not or only obscurely winged, with the keels tapering almost imperceptibly into the hyaline tip or rarely ending in very minute teeth, very finely and shortly rigidly ciliolate on the keels; upper 7-nerved, with 2 on each side of the median nerve usually somewhat short, somewhat scabrid on the keel in the upper fourth. *Lemmas* thinly ciliate about the middle or in the upper two-thirds; lower elliptic-oblong, 3·5–4·5 mm. long; upper ovate to elliptic-ovate, about 3 mm. long, entire and acuminate or minutely notched to 0·5 mm. deep and with a very small mucro (rarely a short awn), usually 1-nerved. *Anthers* 2–2·5 mm. long. *Grains* obovate to obovate-elliptic, 1·5–1·8 mm. long, 1–1·2 mm. wide, reddish brown to blackish purple, embryo-mark often obscure. *Pedicelled spikelets* usually ♂, 4–5·5 mm. long, straw-yellow to pale purplish; glumes almost membranous, lower 8- to 9-nerved, upper 5- to 7-nerved; lemmas well developed; anthers 1·5–2·5 mm. long.

Diagnostic characters and affinities

Sorghum propinquum is distinguished by its few thick rhizomes; tall stout culms, 1–3 cm. wide near the base; numerous leaves with broad blades mostly 3–5 cm. wide; large loose panicles; small narrow acute sessile spikelets, almost elliptic in outline, 3·8–5 mm. long, 1·5–2 mm. wide, usually awnless; the thin glumes, subcoriaceous below and almost papery above the middle; and rather large anthers in comparison with the size of the spikelets. It is separated from *S. controversum* by its stouter culms, wider leaf-blades, and smaller, usually awnless, sessile spikelets. It differs from *S. miliaceum* in the more acute tip of the sessile spikelets and the thinner glumes, with the lower one very finely keeled and not distinctly 3-toothed at the tip.

Distribution and utility

This species has the most easterly distribution of the wild Sorghums belonging to the section *Eu-Sorghum*. It is common in many parts of the Philippine Islands, where the type specimens were collected, and it is also found on many of the islands of south-east Asia, including Palau Islands, the Moluccas, Borneo, Sarawak, and the Malay Islands, as well as on the mainland of southern China, the Malay Peninsula, and Siam. It is also found in southern India and Ceylon, where it may have been introduced. With its tall stout culms, broad leaves, and large panicles, it has the appearance of being much more of a jungle grass than *Sorghum halepense*, resembling *S. miliaceum* in its robustness.

According to Piper (in *Proc. Biol. Soc. Wash.* **28**, 30, 1915) seeds from Manila, Luzon Island, were introduced into the United States, where under cultivation *S. propinquum* was found to resemble the cultivated grain Sorghums in its coarse stems and wide leaves. It also required a long time to reach maturity, for at Biloxi, Missouri, 2-year-old plants did not bloom until the end of October, and at Washington, D.C., the plants had not bloomed before they were cut down by frost, but the rootstocks survived the winter.

It is probably on account of its lateness in maturing, coupled with its thick culms, which would be difficult to cut with machinery, that this species does not appear to have received much attention as a fodder-crop for feeding to stock, in spite of the abundance of its broad leaves. There would also be some difficulty in harvesting the seed, as the racemes are very fragile when mature and a large proportion of the spikelets would probably fall before being harvested.

(i) Var. **propinquum**

Var. **propinquum** is based on *Andropogon propinquum* Kunth, *Rev. Gram.* **1**, Suppl. 40, 1830 and *Enum. Pl.* **1**, 502, 1833, which is based on *A. affinis* J. S. Presl, in C. B. Presl, *Rel. Haenk.* **1**, 343, 1830.

A. sorghum subsp. *halepensis* var. *propinquus* (Kunth) Hack. in *DC., Monogr. Phan.* **6**, 503, 1889, excluding Trimens specimen from Ceylon, has the same basis and is included in this variety.

A. halepensis propinquus (Kunth) Piper in *Proc. Biol. Soc. Wash.* **28**, 29, 1915, rests on the same foundation and is also included here.

This variety has small sessile spikelets 3·8–4·5 mm. long, and 1·2–1·8 mm. wide. Its distribution is mainly east of Siam.

CHINA. Canton: *Hance* 4879! *McClure* 9138! Kwantung: *McClure* 9985! Taipu (Taifu): *Ford* 484! Hainan Island: *Henry* 8295! Paak Po Shan, Toam-chau district (Lignan University 16,236) *Tsang Wai-Tak* 737!

PHILIPPINE ISLANDS. Luzon Island: *Elmer* 8287! *Cuming* 569! *Loher* 1806! 1807! *Merrill* 1468! *Ramos* 13,609! Mindanao Island: *Copeland* 466! *Weber* 1015! Balabac Island: *Vidal* 3996! Without precise locality, *Loher* 7169! 7209!

BORNEO. Bandjarmassin, *Motley* 444! Sarawak State: *Beccari* 3924! *Clemens* 21,308!

MOLUCCAS. Ceram Island: *Kornassi* 448! Buru Island: *Riedel*!

MALAY PENINSULA. Pahang: Sungei Jelei, *Machado* 11,529!

PALAU ISLANDS. Without precise locality, *Lederman* 14,284!

(ii) Var. **siamense** (Piper) Snowden

Var. **siamense** (Piper) Snowden, stat.nov., is based on *Andropogon halepensis siamensis* Piper.

A. halepensis subsp. *siamensis* Piper in *Proc. Biol. Soc. Wash.* **28**, 30, 1915, is based on specimens collected in Siam, the type being *Kerr* 2156 in Kew Herbarium.

This variety has sessile spikelets 4·5–5 mm. long, and 1·8–2 mm. wide. It is found from Siam westwards to southern India and Ceylon.

SIAM. Near Kampang, 106 m., growing in pampas along the banks of Mei Ping River, *Kerr* 2156! Pak Bawag, *Kerr* 2006! Bangkok, *Kerr* 4358! Maneron, Chainat, 50 m., *Kerr* 19,671!

CAMBODIA. Phnom Penk (Oct. 1878) *Godefroy-Lebeuf* 83!

INDIA. Madras: Kodaikanal Ghat and Poombari, *Bourne* 1042! 1896! Tadagam Hills, Coimbatore district, *Fischer* 2693! Without precise locality: *Anamallays*! *Jacob* 17,273! *Wallich Herbarium* 8778D (i).

Jacob's specimen is a very small piece of young material.

CEYLON. Without precise locality, *Thwaites* C.P. 2484!

Regarding *Sorghum affine* A. Camus, in Lecomte, *Fl. Gen. Ind. China*, **7**, pt 2, 321, 1922, it is to be noted that this is not the same as *Sorghum affine* Kuntze, *Rev. Gen. Pl.* p. 791, 1891, which is based on *Andropogon affine* R.Br., *Prod.* **1**, 201, 1810, and has since been named *Dichanthium affine* (R.Br.) A. Camus in *Bull. Mus. Hist. Nat. Paris*, **27**, 548, 549, 1921.

SUBSECTION ARUNDINACEA, SERIES SPONTANEA Snowden
(In *Kew Bull.* p. 223, 1935)

5. **Sorghum virgatum** (Hack.) Stapf

Andropogon sorghum var. *virgatus* Hack. in *DC., Monogr. Phan.* **6**, 504, 1889, is the basis of this species, which is founded on specimens from Egypt and the Anglo-Egyptian Sudan. Of those cited by Hackel I have seen *Kotschy* 173 and *Schweinfurth* 529 and 538.

Sorghum virgatum (Hack.) Stapf in Prain, *Fl. Trop. Afr.* **9**, 111, 1917, is based on *Andropogon sorghum* var. *virgatus* Hack.

Description

A loosely tufted annual 30–150 cm. high. *Culms* slender, mostly 3–6 mm. wide, often with suberect branches from the lower and middle nodes. *Leaves* few; blades narrow, usually 5–15 mm. but sometimes 20 mm. wide, the longer ones attenuated towards the base, with the mid rib stout in robust specimens. *Panicle* very narrow, oblong or elliptic-oblong, 15–60 cm. long, mostly 1–5 cm. wide; branches very slender, erect or suberect, the lower 5–15 cm. long, bare for 1–5 cm. from the base. *Racemes* fragile, few- to 7-noded, up to 4 cm. long; internodes 4–5 mm. long, ciliate with whitish hairs 1–2 mm. long, pedicels similar or a little shorter. *Sessile spikelets* narrowly lanceolate, acute, 6·5–7 mm. long, 2–2·5 mm. wide, pale straw-colour or at length cream to buff yellow, with a few greenish nerves visible above the middle of the lower glume, rarely with purplish colouring, becoming somewhat glossy when mature; callus moderately to densely bearded. *Glumes* coriaceous from near the base to the middle or somewhat above the middle, then subcoriaceous to papery; lower with 11–13 primary nerves, the keels evident from about the middle, narrowly marginate and spinulously ciliolate in the upper third, terminating in minute teeth below the short hyaline tip, generally sparsely strigillose or at length almost glabrous; upper with 7 primary nerves, keeled above the middle, scabrid in the upper third otherwise almost glabrous except for the long-ciliate hyaline margins. *Lemmas* thinly long-ciliate; lower elliptic-oblong, about 5 mm. long; upper ovate-elliptic, 3·5–4 mm. long, with the lobes 0·5–1 mm. deep and a slender awn from the sinus 8–16 mm. long. *Anthers* 2·5–3 mm. long. *Grains* narrowly obovate-elliptic, 2·5–3 mm. long, 1·5–2 mm. wide, reddish brown, embryo-mark distinct. *Pedicelled spikelets* usually ♂, but sometimes reduced, 6–7 mm. long, readily deciduous; lower glume 9-nerved, upper 7- to 8-nerved; anthers about 2 mm. long.

Diagnostic characters and affinities

The long very narrow panicle, with its branches suberect and keeping near to the rhachis, combined with the narrow lanceolate spikelets 6·5–7 mm. long, furnished with long slender awns, generally suffice to enable this species to be distinguished from its nearest relative, *S. lanceolatum*. The latter has a broader panicle as well as wider lanceolate sessile spikelets with stouter awns. When the panicles of *S. virgatum* have been disarranged and the branches spread out, as sometimes happens in pressing and mounting the specimens, they lose their characteristic shape. Both the panicles and the spikelets are usually of a pale straw colour to cream or buff, and it is only rarely that they become tinged with mahogany or brownish purple colour.

Distribution and utility

From the specimens at present available it would appear that the natural distribution of *S. virgatum* is mainly confined to the hotter and drier districts of Egypt and the Anglo-Egyptian Sudan. Chiovenda (in *Fl. Somali*, 2, 438, 1932) also records it from the Juba province of Italian Somaliland. A poor specimen in the Kew Herbarium, however, *Ciеferi* 159, collected in the same province, and from which all the racemes have fallen, has hairy spikelets with stoutish awns like those of *S. lanceolatum*, and it is possible that some of the other specimens from Juba province may belong to this latter species.

S. virgatum was introduced from Egypt into Algeria, where it was grown for fodder under the name of Sorgho Menu. It was recommended by Trabut (in *C.R. Acad. Agric. Fr.* 1916) as a small Sorghum suitable for cultivation in dry regions. Piper (in *Proc. Biol. Soc. Wash.* 28, 33, 1915) states that seed of it obtained from Trabut was introduced into the United States, where it was grown for some years under the name of Tunis Grass. Under cultivation in the United States it behaved purely as an annual and it was found to cross naturally with *S. sudanense* (Piper) Stapf, and the cultivated sweet-stemmed variety known as Amber [a variety of *S. dochna* (Forsk.) Snowden]. Among early references to its cultivation in the United States under the name of Tunis Grass are those of Oakley in 1912 (*U.S. Dep. Agric. Year Book*, pp. 499–501) and Vinall in 1914 (*Farmers' Bull. U.S. Dep. Agric.* no. 605, p. 4). The slender culms, narrow leaves, and fragile racemes, which break up readily and allow the fruiting spikelets to fall so easily at maturity, tend to detract from the usefulness of this species under cultivation and it has been superseded in most districts by taller species with more abundant foliage. Most of the specimens enumerated below have been found in or near cultivated lands, often in sandy soils, but sometimes in irrigated lands.

EGYPT. Near Cairo: Talbia, and the Pyramids, *Acherson* 316! *Bové* 268! 269! 365! *Bolland* (July 1912)! *Keller* 428! *Meinertzhagen*! *Shabetai* 7! Ismailia, Zagazig, and Siüt: *Muschler* (Dec.–Mar. 1904–5)!

ANGLO-EGYPTIAN SUDAN.[1] Between Dongola and Meru, *Bromfield* 32! Between Khartoum and Berber, *Schweinfurth* 529! 538! Kordofan, *Kotschy* 173! Khartoum, *Johnson*! *Aylmer* 322! 408! Without precise locality, *Punter*!

Vern. name. Garawi.

SOUTH AFRICA. Bechuanaland: Mafeking, *Nat. Herb. Pretoria* H. 11,074!

Vern. name: Tunis Grass.

The specimen from Mafeking is mixed with a *Sorghum* sp. near *S. mellitum* var. *australe* Snowden.

WEST AUSTRALIA. Swan River, *Drummond*!

The specimen from West Australia was cited by Bentham (in *Fl. Aust.* **7**, 540, 1878) under *S. halepense* Pers. It agrees well with a specimen from near Cairo, Egypt (*Bové* 268, collected in 1830), and it seems possible that Drummond's label may have been wrongly attached to the specimen.

Hackel (in *DC., Monogr. Phan.* **6**, 504, 1889) cites specimens from Upper Egypt: at Damietta, *Ehrenberg*; Alexandria, *Wichura*; and Suez, *Kotschy It. Syr.* 882, as well as from the Oasis of Thebes, *Unger*; in addition to those given above. He also cites a specimen from Senegal, *Perrottet* 928; but according to Stapf (in Prain, *Fl. Trop. Afr.* **9**, 111, 1917) this is probably *S. lanceolatum*. Stapf also states that, according to the specimens in Forskal's herbarium in Copenhagen, *Holcus exiguus* Forsk. (in *Fl. Aeg.-Arab.* p. 174, 1775) is *Sorghum halepense* (Linn.) Pers. Piper would therefore appear to have been mistaken in identifying Forskal's species with that of *Andropogon sorghum* var. *virgatus* when describing his *A. sorghum exiguus* (in *Proc. Biol. Soc. Wash.* **28**, 32, 1915).

6. **Sorghum lanceolatum** Stapf

Sorghum lanceolatum Stapf in Prain, *Fl. Trop. Afr.* **9**, 112, 1917. This species was described by Stapf from specimens in Kew Herbarium, *Dalziel* 293, collected in the Katagum district of Northern Nigeria, and *Broun* 1473, from the Upper Nile province of the Anglo-Egyptian Sudan.

DESCRIPTION

An annual or short-lived perennial up to 2·5 m. high. *Culms* slender to somewhat stout, 5–10 mm. wide, simple or branched above. *Leaves* many; blades up to 50 cm. long, somewhat narrow, generally not exceeding 2 cm., but sometimes up to 3 cm. wide, often with a rather broad rounded base, the larger ones with the mid rib prominent and acutely keeled below. *Panicle* lanceolate to ovate-oblong, 20–40 cm. long, up to 15 (rarely 20) cm. wide; branches rather slender and flexuous, soon spreading, the lower 10–15 (rarely 25) cm. long, well furnished with spikelets almost to the base. *Racemes* fragile, 2- to 4-noded, up to 3 cm. long; internodes slender, 3–5 mm. long, ciliate with whitish hairs 1–1·5 mm. long, pedicels similar, or a little shorter. *Sessile spikelets* lanceolate, shortly acuminate, 6–8 mm. long, 2–3 mm. wide, cream to buff yellow with a few greenish nerves visible in the tips of the glumes, often turning reddish to maroon when mature, somewhat whitish strigillose or at length almost glabrous; callus copiously bearded with hairs about 1 mm. long. *Glumes* coriaceous below but thinner above the middle; lower 11- to 13-nerved, with the keels distinctly evident in the upper half, obscurely or not winged, finely spinulously ciliolate, and terminating with obscure or very minute teeth below the hyaline tip; upper 7-nerved, sharply keeled and somewhat scabrid in the upper fourth. *Lemmas* thinly long-ciliate; lower lanceolate to elliptic-lanceolate, about 6 mm. long; upper ovate-elliptic, 4–4·5 mm. long, 2-lobed to about 1 mm. deep, awn stoutish, 5–16 (rarely 20) mm. long. *Anthers* 3·5–4 mm. long. *Grains* obovate-elliptic to obovate-oblong, 3–3·5 mm. long, 2–2·5 mm. wide, reddish to brownish, with the embryo mark somewhat obscure. *Pedicelled spikelets* 6–8 (rarely 10) mm. long, often ♂ but sometimes reduced, deciduous; lower glume 9- to 11-, upper 5- to 7-nerved; anthers 3–4 mm. long.

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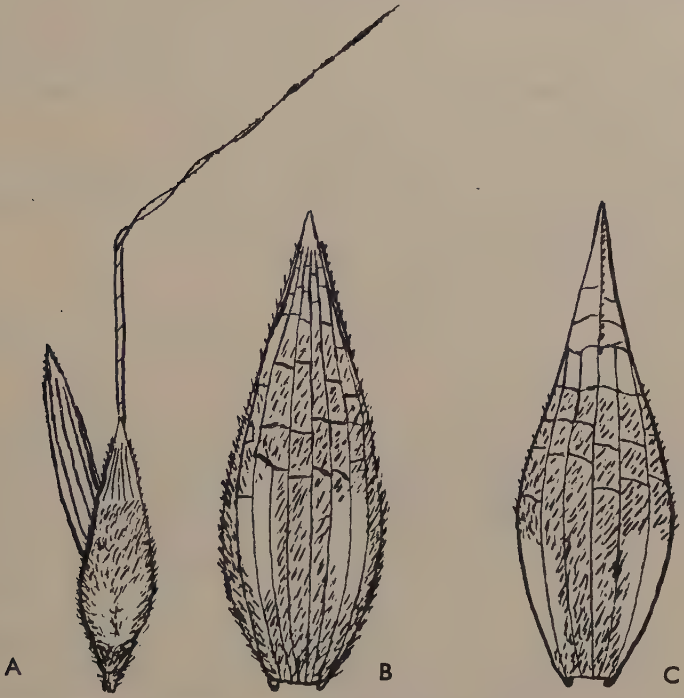
[1] The former Anglo-Egyptian Sudan is now known as Sudan.



Sorghum lanceolatum Stapf. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view. A, × 5; B and C, × 10. (From *Trapnell* 920.)

Diagnostic characters and affinities

In its characteristic features *S. lanceolatum* is somewhat intermediate between *S. virgatum* Stapf and *S. vogelianum* Stapf. From the former it differs in its stout tall culms, larger spreading panicle with flexuous branches, wider sessile spikelets with stoutish awns, and a greater tendency towards reddish or purplish colouring at maturity. It differs from *S. vogelianum* in its smaller and narrower lanceolate sessile spikelets more finely spinulously ciliolate on the keels of the lower glume, and from the typical specimen, collected by *Vogel*, in its narrower leaves. It should be noted, however, that some of the less robust specimens of *S. vogelianum* have rather narrow leaves and differ from *S. lanceolatum* mainly in the wider elliptic- to oblong-lanceolate sessile spikelets coarsely spinulously ciliolate on the keels of the lower glume.

Distribution and utility

S. lanceolatum is most frequent in the southern provinces of the Anglo-Egyptian Sudan, but its distribution also extends westwards through Nigeria and the French Sudan to Senegambia. Specimens have also been collected in northern Uganda and in the Juba province of Italian Somaliland. It has also been introduced into the United States of America, where many plants have been raised from seed collected by Shantz in the Anglo-Egyptian Sudan, but its cultivation in that country does not appear to have passed the experimental stage. It has also been introduced for trial in Northern Rhodesia. A few specimens, collected in Northern Nigeria near fields of cultivated grain Sorghums, have tough racemes and appear to have resulted from intercrossing between the cultivated Sorghums and *S. lanceolatum.* Although it has stouter and more leafy culms that would tend to make it more useful for fodder than *S. virgatum*, it does not appear to have been cultivated for that purpose. It probably requires a warmer climate than some of the Sorghums that are generally grown to feed live-stock. Most of the specimens from Africa that are given below were found growing near to rivers or in swampy lands, but a few were collected in or near to cultivated lands and one in very dry cotton fields.

Senegambia. Without precise locality, *Heudelot* 544! 654!

Both these specimens are somewhat immature.

French Sudan. El Oudladji, *Chevalier* 43,947!

Nigeria. Northern Provinces: Katagum district, *Dalziel* 293! Southern Provinces: Kwarre, *Sampson* 27! Onitsha, *Jones* 6277!

Vern. name: Dawar Rafi.

The following specimens with tougher racemes and rather wider sessile spikelets have probably resulted from intercrossing between this species and a cultivated grain Sorghum such as *Sorghum guineense* Stapf: Kwarre, *Sampson* 25! 26! Onitsha, *Jones* 6887!

Anglo-Egyptian Sudan. Upper Nile province: White Nile, Kio Rubber Plantation, *Broun* 1473! Mongalla province:[1] Malakal, *Shantz* 966! 967! 968! *Simpson* 7440! Taufikia, *Shantz* 959! mouth of Sobat River, *Shantz* 962! *Evans Pritchard* 32! Rejaf, *Shantz* 947! 948! 949! 950! Nimule, *Shantz* 895! 899! Tendelai, Gash Delta, *Andrews* 10! s.n.!

Two poor specimens collected at Mongalla and Nimule, *Simpson* 7600! 7568! probably belong here. Also a vigorous specimen with rather larger spikelets than usual, *Myers* 7326! collected on the River Sire, Meridi district.

Vern. names: Adar (Arabic); Abet (Dinka); Obaro (Anuak); Titavunde (Zande); Ngorinye-Lokima (Kakwa); Neibel (Mberedi); Nuku Su (Mve Gumba).

In addition to the above, there are a large number of specimens from plants grown mainly in greenhouses at experimental stations in the United States from seed collected by *Shantz* in the localities named above. These were sent to Kew by the United States Department of Agriculture Sorghum Herbarium. The most typical are S.P.I. numbers: 02093! 51995! 51997! 51998! 52002! 52004! 52006! 52021! 52026! 52028! 52031! 52032! 52035! 52037! 52039! 52042! 52045! 52046! 52051! 52068! 52069! 52073! 52074! 52077! 52080! 52081! 52082! 52083! 52085! 52094! 52098! 52101! 52102! 52103! 52109! 52114! 52116! 52117! 52118! 52155! 52159! 52160! 52161! 52163! 52166!

Most of the sessile spikelets have fallen off the specimens and are enclosed in envelopes attached to the mounting sheets.

The following have unusually wide leaves, which may be due either to the conditions under which the plants were grown or in some cases to intercrossing with wider-leaved species: S.P.I. numbers: 52016! 52017! 52018! 52019! 52020! 52022! 52023! 52024! 52049! 52050! 52093! 52097! 52099! 52100! 52104! 52105! 52107! 52108! 52110! 52112! 52113! 52158! 52164!

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[1] Mongalla province is now known as Equatoria.

ITALIAN SOMALILAND. Juba province, *Cifeiri* 159!
This is a poor specimen, with all the spikelets fallen from the panicle.
UGANDA. Chua district, at Kitgum, *Thomas* 4349!
NORTHERN RHODESIA. Mazabuka, under trial for fodder purposes, *Trapnell* 920!

7. **Sorghum vogelianum** (Piper) Stapf

Andropogon sorghum vogelianus Piper in *Proc. Biol. Soc. Wash.* **28**, 34, 1915, is the basis of this species. The type specimen cited by Piper is *Vogel* 11 in Kew Herbarium. It was collected on the banks of the Nun River, Southern Nigeria. Piper mentions other specimens but states that although very similar none of them matches Vogel's plant.

Sorghum vogelianum (Piper) Stapf in Prain, *Fl. Trop. Afr.* **9**, 116, 1917. Based on *Andropogon sorghum vogelianus* Piper.

DESCRIPTION

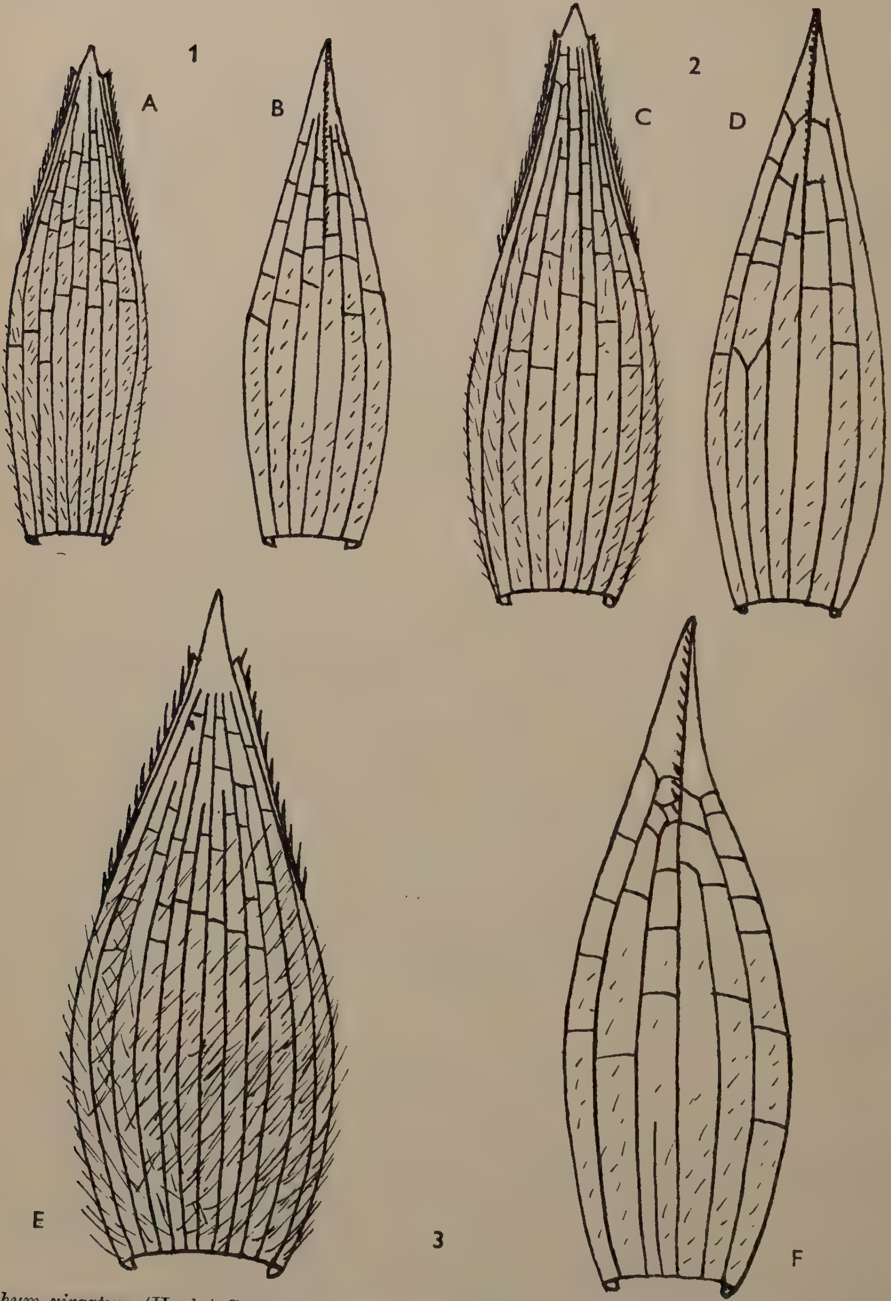
A tall loosely tufted annual, or sometimes perennial, 2–5 m. high. *Culms* stout, up to 1 cm. wide, usually simple. *Leaves* many; blades up to 75 cm. long, 3–7 cm. wide in vigorous specimens, but only 1–2 cm. wide in depauperate specimens, with a broad rounded base, tapering upwards to an acuminate tip. *Panicle* large and loose, elliptic or pyramidal, 15–45 cm. long, 5–25 cm. wide; branches obliquely ascending or spreading, slender and flexuous except near the villous base, the lower 5–20 cm. long, furnished with spikelets throughout, or bare for 1–5 cm. *Racemes* fragile, 2- to 7-noded, up to 3·5 cm. long; internodes slender, 3–4 mm. long, densely ciliate with fulvous or rufous hairs 1–1·5 mm. long; pedicels similar, 3–5 mm. long. *Sessile spikelets* elliptic- to oblong-lanceolate, acuminate, 8–9 (rarely 7–10) mm. long, 2·5–3·5 mm. wide, straw colour to buff yellow or at length tawny to red or black; awned or awnless; callus densely bearded with hairs about 1 mm. long. *Glumes* coriaceous to beyond the middle, thinner above with the greenish nerves visible; lower with 12–15 primary nerves, a few cross nerves near the middle, 2-keeled from the middle upwards with the sharp keels narrowly winged and coarsely spinulously ciliate, terminating in minute teeth near the tip, hairy with fulvous to rufous hairs, especially at the base and sides, or at length glabrescent on the back; upper with 7 primary nerves, a few cross-nerves in the upper two-thirds, scabrid on the keel in the upper third, glabrous or sparsely hairy. *Lemmas* densely ciliate; lower elliptic-lanceolate, 7–8 mm. long; upper ovate, 4–5 mm. long, 2-lobed to 1·5 mm. deep, with an awn 8–16 mm. long, or subentire and mucronate or with a short bristle. *Anthers* 4–5 mm. long. *Grains* obovate-elliptic, about 3·5 mm. long and 2 mm. wide, tawny to dark-red. *Pedicelled spikelets* ♂ or sometimes neuter, 7–9 mm. long, at length deciduous; lower glume 10- to 11-nerved, upper 5- to 7-nerved; anthers about 4 mm. long.

DIAGNOSTIC CHARACTERS AND AFFINITIES

S. vogelianum is most closely related to *S. lanceolatum*, but the typical specimens are readily separated from the latter species by the wide leaves, very large panicles, and the larger sessile spikelets. Some specimens, however, have rather narrow leaves and small panicles, due either to unfavourable conditions of growth, or because they have been collected from tiller-shoots or from secondary branches. These can generally be distinguished from *S. lanceolatum* by the larger elliptic- to oblong-lanceolate sessile spikelets with long coarse spinulous cilia on the keels of the lower glume.

DISTRIBUTION AND UTILITY

The distribution of this species, as at present known, is limited to Nigeria and the Cameroons, but it is possible that it may extend into some of the adjacent territories of West Africa. The material available at Kew is very small and there is no information as



(1) *Sorghum virgatum* (Hack.) Stapf. A, lower glume; B, upper glume. (From *Schweinfurth* 529.) (2) *S. lanceolatum* Stapf. C, lower glume; D, upper glume. (From *Dalziel* 293.) (3) *S. vogelianum* (Piper) Stapf. E, lower glume; F, upper glume. (From *Vogel* 11.) All ×10, exterior view.

to the plants being used for any special purpose. As it grows in a region where the climate is hot and humid, it is unlikely to prove suitable for cultivation as fodder in most of the countries devoted to stock-raising on a large scale. Most of the plants listed below were found growing on the banks of rivers, and there is no evidence that they frequent cultivated lands.

NIGERIA. Northern Provinces: without precise locality, *Lely* 778! Southern Provinces: on the banks of the Nun River entrance to the River Niger, *Vogel* 11! Idu, banks of the Eugenni River, *Holland* 153! Makurdi, north bank of river, *Sampson* 37!

CAMEROONS. By the Cameroon River, *Mann* 2109!

In addition to the above Stapf cites the following: Southern Nigeria, Lau and Amar, by the Benue River, *Macleod* 49, 60, 62, 65; Oban, *Talbot* 846; Cameroons, Karnak Logome, *Macleod* 157.

Among the specimens mentioned by Piper under his *Andropogon sorghum vogelianus* (in *Proc. Biol. Soc. Wash.* **28**, 34, 1915), but excluded by Stapf (in Prain, *Fl. Trop. Afr.* **9**, 116, 1917), two in Kew Herbarium, *Mahon*, collected in Uganda in 1902, and *Kirk*, collected below Mazzaro on the Zambesi River in 1860, are now referred to *Sorghum verticilliflorum* Stapf. The specimens in Herb. Berol. cited by Piper have not been seen by me, but those from Tanganyika Territory (German East Africa) are unlikely to belong to *S. vogelianum*, which is a West African species. The specimen cited by Piper from Korbo, on the Chari River, near Lake Chad, *Chevalier* 9397, is within reasonable range of the area of distribution and is probably a form of *S. vogelianum*.

8. **Sorghum aethiopicum** (Hack.) Rupr. ex Stapf

Andropogon sorghum var. *aethiopicus* Hack. in *DC., Monogr. Phan.* **6**, 504, 1889, is the foundation of this species. It was described by Hackel from plants collected by Kotschy and Schweinfurth in the Anglo-Egyptian Sudan. Of those cited by Hackel I have seen *Kotschy* 132 and 390.

Sorghum aethiopicum (Hack.) Rupr. ex Stapf in Prain, *Fl. Trop. Afr.* **9**, 119, 1917, rests on *Andropogon sorghum* var. *aethiopicus* Hack.

DESCRIPTION

An annual 0·5–3 m. high. *Culms* slender to stout, 0·5–2 cm. or more wide, simple or branched above. *Leaves* few to many; blades lanceolate to linear-lanceolate, 5–35 cm. long, 0·5–3 cm. wide, the short ones with a broad rounded and subcordate base, the longer ones somewhat narrowed towards the base, the midrib rather slender. *Panicle* narrow, linear to elliptic-oblong, 10–40 cm. long, 3–10 cm. wide, contracted or loose below, sometimes subsecund; branches usually 2–3 from each node, suberect and flexuous except near the villous base, 5–10 (rarely 20) cm. long, divided near the base or bare for 1–5 cm. *Racemes* more or less fragile, 1- to 4-noded, up to 2·5 cm. long; internodes slender, 3–5 mm. long, densely ciliate with white hairs 1 mm. long; pedicels very similar but sometimes shorter. *Sessile spikelets* elliptic- to ovate-lanceolate, acute or subacute, 6–8 mm. long, 2·5–3·5 mm. wide, pale cream to buff yellow or somewhat tawny to reddish, especially near the tips and below the middle, permanently and densely white-tomentose or sometimes becoming glabrescent on the more exposed portions, long-awned; callus beard copious. *Glumes* coriaceous almost throughout but thinner towards the tips where the nerves become visible; lower 13- to 15-nerved, the keels narrowly winged and spinulously ciliolate in the upper third, terminating in minute teeth, with the hyaline apex projecting between them; upper 7-nerved, the keel sharp and scabrid in the upper third. *Lemmas* densely ciliate; lower elliptic-oblong, 6–7 mm. long; upper ovate, 4·5–5 mm. long, 2-lobed for 1·5–2 mm. deep, awn stoutish, usually 20–30 mm. long. *Anthers* 3·5–4 mm. long. *Grains* obovate-elliptic, 2·5–4 mm. long, 1·5–2 mm. wide, tawny to dark red, embryo-mark usually distinct. *Pedicelled spikelets* usually ♂ but sometimes reduced, 7–9 mm. long, often more or less reddish coloured, tardily deciduous; lower glume 8- to 10-nerved, upper 5- to 7-nerved; anthers 3–4 mm. long.

Diagnostic characters and affinities

S. aethiopicum is characterized by the narrow panicles of densely hairy long-awned sessile spikelets 6–8 mm. long, 2·5–3·5 mm. wide. In specimens having rather narrow spikelets it approaches near to *S. lanceolatum*, but usually it can be distinguished from it by the narrower panicle, the more densely hairy elliptic-lanceolate sessile spikelets, and the longer awns; also the leaves are generally wider in comparison with their length. Some of the less hairy specimens may resemble *S. macrochaeta* (*S. abyssinicum* Stapf non Kuntze), but the latter has a larger, wider, and looser panicle and the sessile spikelets shortly and finely hairy with usually tawny hairs, or the spikelets may be almost glabrous; the leaf-blades are also much longer and wider.

Distribution and utility

This species is widely distributed in the Anglo-Egyptian Sudan. It also extends westwards to Northern Nigeria and the French Sudan and eastwards to Eritrea and British Somaliland. A specimen has also been recorded from the Tana River region of north-eastern Kenya. A plant found growing in a nursery in Sierra Leone was probably introduced. Although *S. aethiopicum* does not appear to have been much cultivated for fodder there is evidence that it readily intercrosses with some of the cultivated grain Sorghums, especially those of the subseries *Durra*, as specimens that appear to have resulted from such cross-pollination are frequently encountered. A race that has probably arisen from cross-fertilization of this kind has been cultivated to some extent in the United States of America, under the name of *S. hewisonii* (Piper) Longley, and will be described below towards the end of this revision.

S. aethiopicum is most commonly found growing in fertile soils, often close to rivers, near cultivated lands where Sorghums and other crops are grown. It is less frequent in drier sandy or rocky places and plants growing in such habitats are usually small and have narrow sparsely branched panicles. The occurrence of dwarf and tall varieties in this species is something like that of varieties of different height frequent among the cultivated grain Sorghums. In such cases the dwarf varieties are usually preferred for cultivation as they are generally early maturing and more easily harvested.

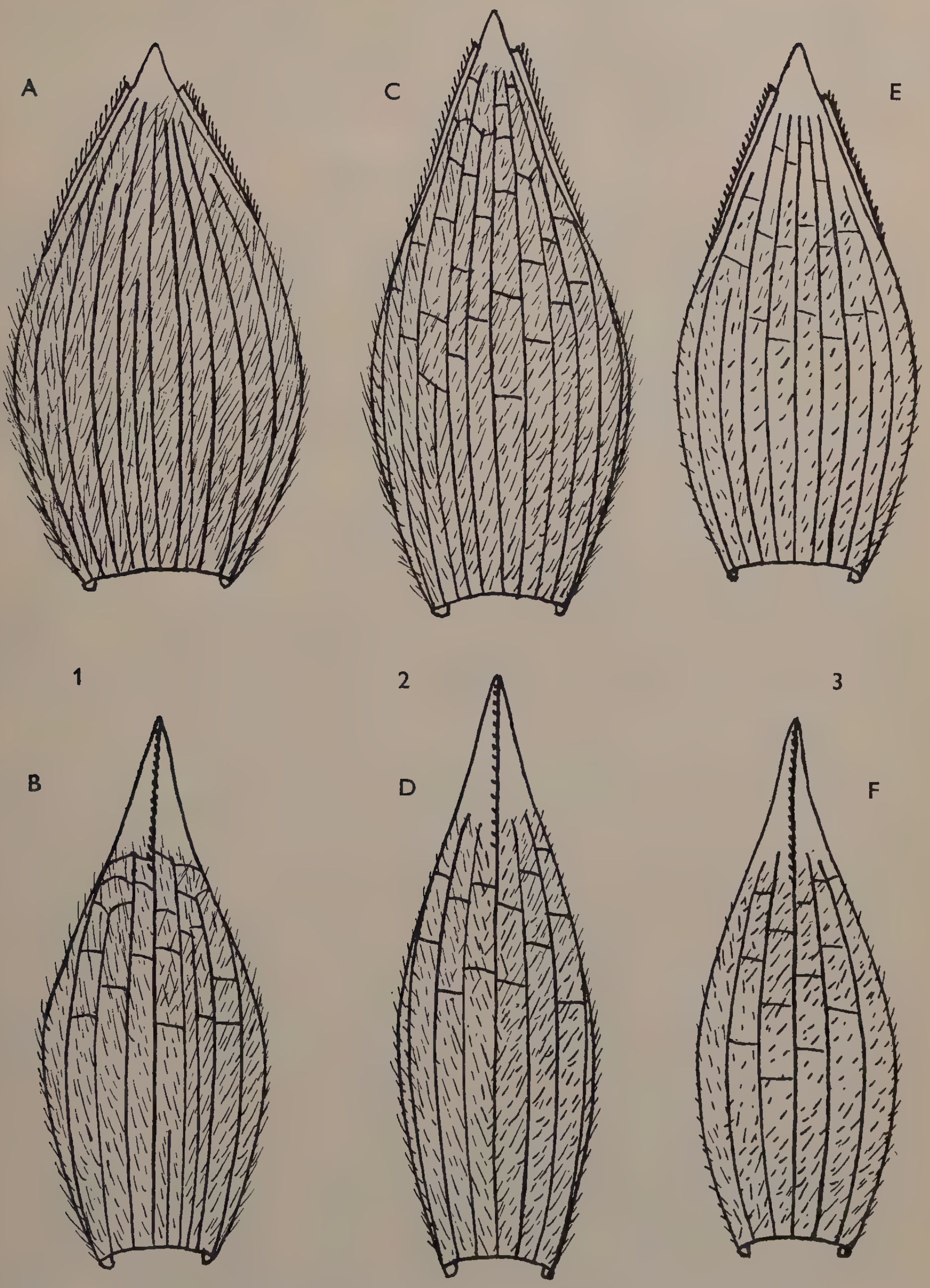
(i) Var. **aethiopicum**

Var. **aethiopicum** is based on *S. aethiopicum* (Hack.) Rupr. ex Stapf. It is described by Hackel as *Andropogon sorghum* var. *aethiopicus* subvar. *longiaristatus* in *DC., Monogr. Phan.* **6**, 505, 1889. Under it Hackel cites *Kotschy* 390, from Jebel Arash-Kol, and *Schweinfurth* 655, from Wadi Eremit. I have seen *Kotschy* 390 in Kew Herbarium.

Culms rather stout and tall, mostly 1·5–3 m. high; leaf-blades linear-lanceolate, from a somewhat narrowed base, tapering upwards to the acuminate tip, mostly 15–35 cm. long and 1·5–3 cm. wide; sessile spikelets 3–3·5 mm. wide, usually with more or less reddish tips; pedicelled spikelets also reddish.

Sierra Leone. Njala, in nursery, probably introduced, *Deighton* 772!

Anglo-Egyptian Sudan. Kordofan, Arash-Kol Mountain, *Kotschy* 390! Blue Nile, *Muriel* L. 13! Gash Delta, Tendelai and Hadeleia, *Andrews* 5! 6! 13! 16! 17! 18! Gedaref and Daysa, *Andrews* A 3273! A3295! Jebel Maya, *Andrews* A3307! Nagam El Dein, *Andrews* 3321! Between Abu Hasleim and Karkoj, *Andrews* A3343! Khor Remeilo, *Andrews* A3353!



(1) *Sorghum aethiopicum* (Hack.) Rupr. ex Stapf var. *aethiopicum*. A, lower glume; B, upper glume. (From *Kotschy* 390.) (2) *S. aethiopicum* (Hack.) Rupr. ex Stapf var. *brevifolium* Snowden. C, lower glume; B, upper glume. (From *Kotschy* 132.) (3) *S. macrochaeta* Snowden. E, lower glume; F, upper glume. (From *Schweinfurth* 1521.) All × 10, exterior view.

Vern. names: Adar, Addar (Arabic, also used for *Sorghum halepense*).

The following specimens, with somewhat tougher racemes, as well as larger leaves and panicles, have probably resulted from intercrossing with cultivated races, but are best placed here: Gash Delta, Tendelai, *Andrews* 4! 8! Upper Nile province, between Buffalo Cape and Kilo 60, Bahr el Jebel, *Harrison* 40!

British Somaliland. Without precise locality, *Collenette* 159!

(ii) Var. **brevifolium** Snowden

Var. **brevifolium** Snowden, var.nov. Culmi gracili, pumili, fere 0·5–1 m. alti; laminae foliorum plerumque 5–10 cm. longae, 0·5–1·5 cm. latae, nonnunquam longiorae, plerumque lanceolatae, basin versus rotundatae vel subcordatae; spiculae sessiles 2·5–3 mm. latae, fere pallido-coloratae, raro apicibus pallido-rubrae; spiculae pedicellatae pariter sessilibus coloratae.

Culms slender and dwarf, mostly 0·5–1 m. high; leaf-blades usually 5–10 cm. long and 0·5–1·5 cm. wide, generally lanceolate, with a broad, rounded or subcordate, base; sessile spikelets 2·5–3 mm. wide, usually pale coloured with greenish nerves showing near the tips; pedicelled spikelets also mostly pale with greenish nerves, rarely with pale reddish colouring.

The type of this variety is *Kotschy* 132 in Kew Herbarium.

French Sudan. Without precise locality, *Chevalier* 43,027!

Northern Nigeria. Kalkala, south-west corner of Lake Chad, *Golding* 77! This is a poor specimen.

Anglo-Egyptian Sudan. Without precise locality, *Kotschy* 132! El Ghazalan, *Punter*! Gezira Research Farm, *Andrews* K31! Gash Delta, Tendelai and Hadeleia, *Andrews* 7! 11! 15! Gedaref, *Andrews* A3238! A3252! Nagm El Dein, *Andrews* 3322!

Kenya Colony. Tana River province, Taneta, 762 m., *Sampson* 95!

In addition to the subvar. *longiaristatus*, Hackel (in *DC.*, *Monogr. Phan.* **6**, 505, 1889) also described a subvar. *breviaristatus*, and cited the following specimens under it: *Kotschy* 158 from Arash-Kol, *Pfund* (in exped. Colston Herb. Berol. 560) from Darfur province, *Schweinfurth* 599 from Sagadi between Suakin and Berber, and a form with dark purple spikelets, *Marloth* 1363 from Damaraland. He also mentions as intermediate between var. *aethiopicus* and var. *virgatus* specimens from Nubia province collected by Hartmann, and as intermediate between var. *effusus* and var. *aethiopicus* a specimen from Matamma, *Schweinfurth* 1521, which he had already cited under var. *effusus* (loc. cit. 504). Of these specimens Stapf included under *S. aethiopicum* only *Schweinfurth* 599. In his footnotes to the species Stapf (in Prain, *Fl. Trop. Afr.* **9**, 120, 1917) states that *Kotschy* 158 has a rather dense panicle and broad spikelets with somewhat triangular subherbaceous tips. He suggests that it may be a cross between *S. aethiopicum* and the cultivated *S. durra*.

Piper, who apparently examined all the above specimens, states (in *Proc. Biol. Soc. Wash.* **28**, 40–41, 1915) that the two specimens collected by Hartmann are infested with ‘Smut Disease’ and are abnormal. He expresses the opinion that the specimen collected by Pfund may be a cultivated plant, or a hybrid with one, and considers it impossible to include it under *cordofanus* (i.e. *aethiopicus*). He is still more doubtful of the specimen collected by Marloth in Damaraland. On the other hand, Piper states that a specimen from the Anglo-Egyptian Sudan, *Broun* 1473, is very close to typical *cordofanus*. This latter specimen, however, is one of the two plants on which Stapf afterwards based his *S. lanceolatum*.

As Stapf pointed out (in Prain, *Fl. Trop. Afr.* **9**, 120, 1917) the use of the name *Andropogon sorghum cordofanus* by Piper for *Sorghum aethiopicum* was due to a mistaken identification, which may have resulted from a confusion of labels, with *Andropogon cordofanus*

Hochst. (*Kotschy* 54) which is *A. gayanus* var. *cordofanus*. Although Stapf drew attention to this mistake he inadvertently included *A. aethiopicus* Rupr. ex. Steud. (which is a synonym of *A. cordofanus* Hochst.) in the synonomy given at the end of his description of *Sorghum aethiopicum*. The latter species is a manuscript name of Ruprecht mentioned in synonomy by Hackel (loc. cit. 504) under *Andropogon sorghum* var. *aethiopicus*. The specimen collected at Matamma, *Schweinfurth* 1521, is the type of *A. sorghum abyssinicus* Piper and will be referred to again under *Sorghum macrochaeta* (*S. abyssinicum* Stapf non O. Kuntze).

9. **Sorghum macrochaeta** Snowden

Andropogon sorghum abyssinicus Piper in *Proc. Biol. Soc. Wash.* **28**, 39, 1915, was described from a specimen collected in the south-east corner of Kassala province in the Anglo-Egyptian Sudan, at Matamma near Gallabat, close to the border of Abyssinia. I have seen the duplicate of the type specimen, *Schweinfurth* 1521.

Sorghum abyssinicum Stapf in Prain, *Fl. Trop. Afr.* **9**, 118, 1917, is based on *Andropogon sorghum abyssinicus* Piper.

Sorghum macrochaeta Snowden in the *Cultivated Races of Sorghum*, p. 237, 1936. This is a change of name for *S. abyssinicum* Stapf. because the latter is invalidated by the older *S. abyssinicum* (R.Br.) O. Kuntze in *Rev. Gen.* p. 791, 1891.

DESCRIPTION

A tall annual or, under favourable conditions, sometimes perennial. *Culms* stout, 5–8 mm. wide at the base of the panicle, often somewhat purplish below the nodes. *Leaves* numerous; blades linear-lanceolate, from a somewhat rounded base long-tapering upwards to a fine point, up to 75 cm. long and 3–6 cm. wide, green with purplish markings, the mid rib rather stout and prominent below in the basal portion. *Panicle* obovate-lanceolate, elliptic, or oblong, loose, up to 35 cm. long and 8–15 cm. wide; branches slender, somewhat flexuous and spreading, the lower ones mostly 5–6 from a node and up to 15 cm. long, usually bare of spikelets for 1–5 cm. from the hirsute base. *Racemes* mostly 2- to 3-noded, up to 2·5 cm. long; internodes and pedicels slender, 4–5 mm. long, shortly ciliate with whitish to fulvous hairs. *Sessile spikelets* elliptic-lanceolate to elliptic-oblong, acute, 6·5–8 mm. long, 2·5–3·5 mm. wide, dull cream to buff yellow when young, with 5–6 nerves evident between the keels of the lower glume, long-awned; callus copiously bearded with hairs about 1 mm. long. *Glumes* coriaceous below the middle, subcoriaceous above; lower 11- to 13-nerved, sharply keeled from just above the middle, with the keel margins slender below but gradually widening upwards until they end in distinct minute teeth below the acute hyaline tip, covered throughout with usually fulvous hairs or becoming glabrescent on some of the more exposed portions; upper 7-nerved, sharply keeled above the middle, scabrid on the keel, sparsely hairy, ciliate on the incurved margins. *Lemmas* finely ciliate; lower elliptic-oblong, 5–6·5 mm. long; upper ovate, 4–5 mm. long, 2-lobed to 1½–2 mm. deep, awn usually 20–25 mm. long. *Anthers* 4–5 mm. long. *Grains* obovate-elliptic, 2·5–4 mm. long, 1·3–2 mm. wide, embryo-mark more or less distinct. *Pedicelled spikelets* usually ♂, 7–8 mm. long, greenish, or often tinged with reddish purple, at length deciduous; lower glume 8- to 10-nerved, upper 6- to 7-nerved; anthers 3–4 mm. long.

DIAGNOSTIC CHARACTERS AND AFFINITIES

S. macrochaeta is distinguished by its long wide leaves; large spreading panicle; and the elliptic-lanceolate to elliptic-oblong sessile spikelets, 6·5–8 mm. long, 2·5–3·5 mm. wide, shortly hairy or at length glabrescent, with long awns usually 20–25 mm. long. It differs from the closely related *S. aethiopicum* in its longer wider leaves, larger spreading panicle, and less hairy spikelets. It is also related to *S. arundinaceum* and *S. verticilliflorum* but may be separated from the former by the long-awned, wider and more elliptic-oblong sessile spikelets; and from the latter by the broader leaves and somewhat larger, wider sessile spikelets with usually longer awns. The margins of the keels of the lower glume of *S. macrochaeta* usually tend to become wider upwards with more distinct minute teeth than do those of the other two species.

DISTRIBUTION AND UTILITY

S. macrochaeta has been recorded in various localities from the southern part of Kassala province in the Anglo-Egyptian Sudan southwards through Mongalla province and the south-eastern areas of the Belgian Congo and the adjoining districts of Tanganyika into Northern Rhodesia. Eastwards it extends into Eritrea. According to Schweinfurth's notes on the type specimen it is a troublesome weed in cultivated lands. There is no evidence available of its cultivation for the purpose of fodder, but plants have been raised and grown experimentally in the United States of America from seed collected in the Anglo-Egyptian Sudan and the Belgian Congo. With its sturdy culms and broad leaves it has the appearance of being a useful fodder plant but it does not seem to be very abundant. It may require a hotter and more humid climate than some of the other species which are more frequently cultivated in stock-breeding countries.

The majority of the specimens listed below were found growing in alluvial soils near rivers or lakes, often in or near cultivated lands. It is evident from the number of intermediate forms between this species and cultivated grain Sorghums that it readily intercrosses with them in all the regions into which it extends.

BELGIAN CONGO. Urua district: Lake Kisale, at Kadia, *Shantz* 596! 597! Kayombe, *Shantz* 602! Bukama, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 49,697! 49,698! Nionga (Nianzu?), ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 50,008! Urundi district: *Ngano Ngano and Nyanza*, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 50,008! 50,790! 50,802! 50,805! 50,806! 50,807! Maniema district: Kasongo, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 50,079!

The following specimens raised in the United States from seed collected in Urundi district at Nyanza, although they have somewhat shorter awns, are best placed here: ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 50,791! 50,792! 50,794! 50,796! 50,801! 50,808! F.C. I. 11,521!

ANGLO-EGYPTIAN SUDAN. Kassala province: near Gallabat, *Schweinfurth* 1521! Gedaref, *Andrews* A3162! 3212! 3232! 3239! Mongalla province: Bahr el Gebel, *Simpson* 7280! Yei River, at Lado, *Sillitoe* 25! Nimule, *Shantz* 896! Rejaf, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 51,999! 52,033! 52,106! 52,111! 52,154! Without precise locality, *Punter*!

Andrews's specimens are unusually hairy and appear to have been grown in a very dry district.

Vern. names: Addar, Adar el Bousse (Arab.).

The following specimens with persistent sessile spikelets, shorter awns, and larger grains, appear to have resulted from intercrossing between this species and cultivated grain Sorghums: Mongalla province: Taufikia, *Shantz* 958! Mongalla and Rejaf, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 52,044! 52,075!

ERITREA. Without precise locality, *Terraciano et Pappi* 2355! The spikelets of this specimen are immature and rather small.

TANGANYIKA TERRITORY. Unyamwezi district, Wala River, *Böhn* 101! Ugogo district, Shinyanga, near River Ninghua and other rivers, 1150 m., *Burtt* 2580!

The following specimens with tough racemes appear to be hybrids between this species and cultivated grain Sorghums: Huru Huru, *Staples* 433! Mpwapwa, *Hornby* 521! Lake Victoria, near Smith Sound, *Rounce* 282!

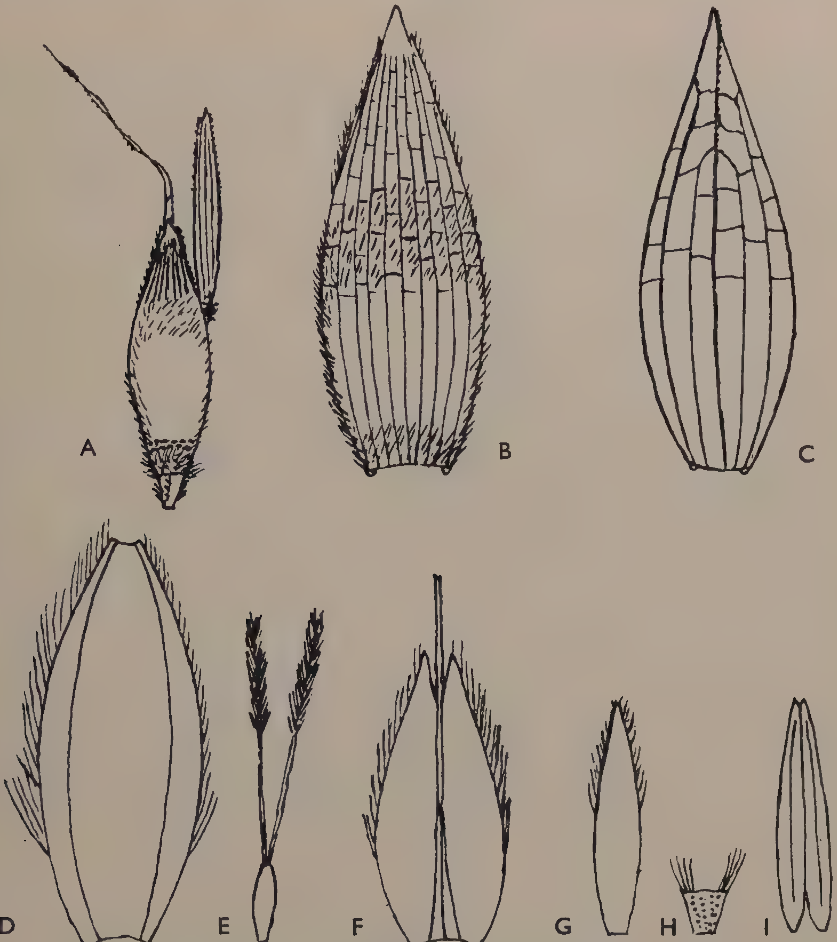
NORTHERN RHODESIA. River Kafue, plains near Mazabuka, *Trapnell* 1092!

SOUTHERN RHODESIA. Deka River, Wankie, *Eyles* 7966!

10. **Sorghum arundinaceum** (Desv.) Stapf

Andropogon arundinaceus Willd., *Sp. Pl.* **4**, 906, 1805, is founded on a specimen collected by Isett in the Guinea region of West Africa. The name is a later homonym of *A. arundinaceus* Bergius, Descr. Pl. Cap. 356, 1767.

Rhaphis arundinacea Desv., *Opusc.* p. 69, 1831, is a different and legitimate generic combination used for *Andropogon arundinaceus* Willd.



Sorghum arundinaceum (Desv.) Stapf. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view; D, lower lemma; E, young ovary with styles and stigmas; F, upper lemma with lower part of awn; G, palea; H, one of the two lodicules; I, an anther. A, × 5; B–I, × 10. (From Herb. *Willdenow* 18,639.)

A. sorghum var. *effusus* Hack. in *DC., Monogr. Phan.* **6**, 503, 1889 (in part; excluding the specimens cited by Hackel from East and South Africa), is based on *A. arundinaceus* Willd.

Andropogon sorghum effusus Piper in *Proc. Biol. Soc. Wash.* **28**, 35, 1915, has the same basis.

Sorghum arundinaceum (Desv.) Stapf in Prain, *Fl. Trop. Afr.* **9**, 114, 1917, is based on *Andropogon arundinaceus* Willd. (non Berg., i.e. *Rhaphis arundinaceus* Desv.).

I have seen a fragment of the type specimen from Guinea, No. 18,639 in Herb. Willdenow. After examining the additional Sorghum material received at Kew from

Africa since Stapf's account of the African Sorghums was published, as well as the specimens in Kew herbarium cited by him and Piper, there is no reason to doubt that Stapf's concept of *Sorghum arundinaceum* agrees with that of *Andropogon arundinaceus* Willd. as far as the West African specimens I have seen are concerned, but I consider that most of the specimens from East and South Africa cited by Stapf are better placed under either *Sorghum verticilliflorum* or *S. macrochaeta.*

Description

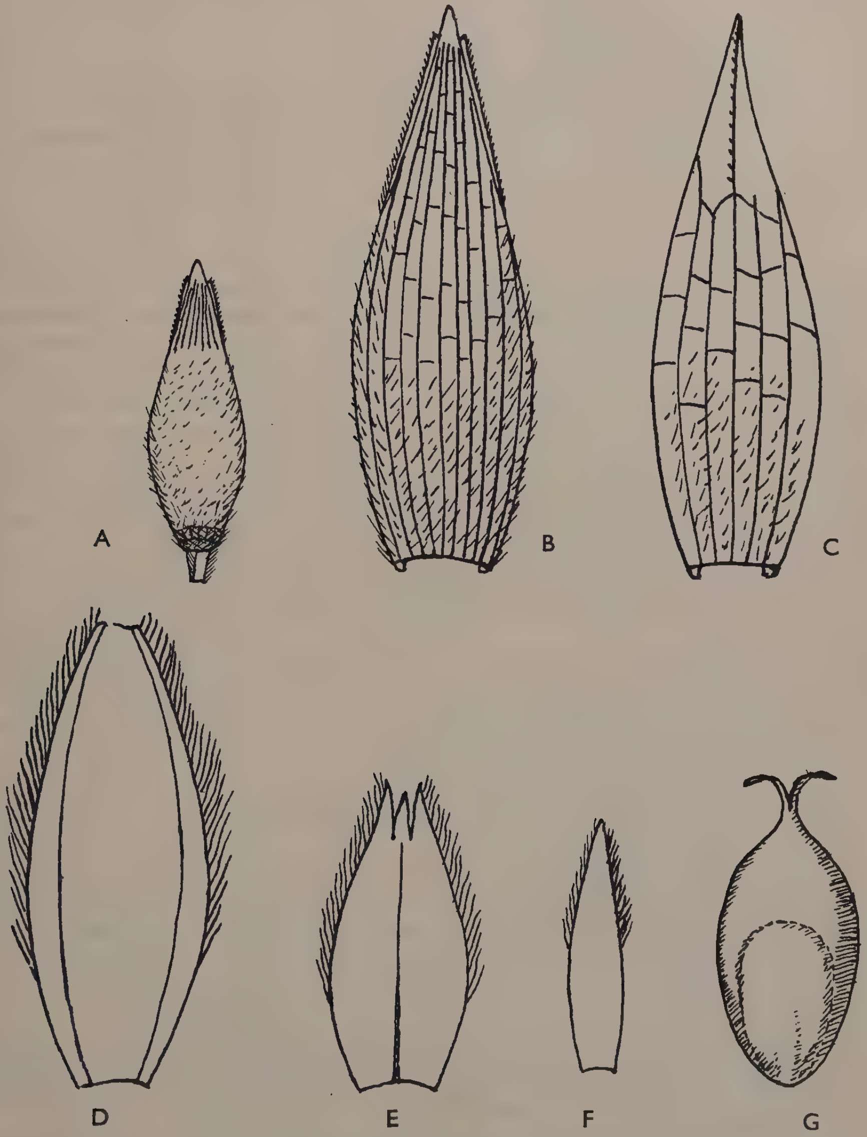
A tall annual or tufted perennial 2–4 m. high. *Culms* stout, usually 1 cm. or more wide, often purplish below the nodes. *Leaves* many; blades linear, from a broad rounded base, narrowing upwards to the slender pointed apex, up to 75 cm. long, 2–6 cm. wide, mostly bright green, often flushed with purple, with a stout tapering mid rib. *Panicle* ovate to elliptic-oblong, loose, 20–60 cm. long, 10–25 cm. wide; branches often 5–8 from each of the lower nodes but reduced to 2–3 in depauperate specimens, obliquely ascending or spreading, slender and flexuous, the lower often 15–30 cm. long, usually undivided for 5–10 cm. or more from the villous base. *Racemes* fragile, 2- to 5-noded, up to 2·5 cm. long, internodes slender, 3–5 mm. long, densely ciliate with fulvous hairs up to 1·5 mm. long; pedicels similar but sometimes shorter. *Sessile spikelets* elliptic- to oblong-lanceolate, narrowly acuminate, 6–7·5 mm. long, 2–2·5 mm. wide, pale cream to straw-yellow or at length tawny to red or black, with 5–6 nerves showing between the keels near the tip of the lower glume, with a short awn or often awnless; callus beard copious. *Glumes* equal, coriaceous and often glossy to beyond the middle, somewhat papery above; lower with 12–16 primary nerves, numerous cross-nerves in the upper two-thirds, keeled in the upper third, with the keels finely margined, spinulously ciliolate and often terminating in minute teeth, more or less densely hairy with tawny to purplish hairs or sometimes becoming somewhat glabrous on the more exposed parts; upper with 7 primary nerves, many cross-nerves above the basal third, keeled above the middle, sharply in the upper third where it is usually scabrid, sparsely hairy on the back and sides. *Lemmas* finely long-ciliate; lower elliptic-lanceolate, 4·5–6 mm. long; upper elliptic-ovate to ovate, 3–4·5 mm. long, 2-lobed to 0·5–1 mm. deep and with an awn 5–10 mm. long, or often subentire and mucronate or with a short bristle. *Anthers* usually 3–3·5 mm. long. *Grains* obovate-elliptic to obovate, 2–3 mm. long, 1·5–2 mm. wide, yellowish brown to dark red or almost black; embryo-mark somewhat obscure. *Pedicelled spikelets* ♂ or sometimes neuter, 5–8 mm. long, somewhat greenish to purplish, at length deciduous, linear-lanceolate, acute; lower glume 9- to 11-nerved, upper 5- to 7-nerved.

Diagnostic characters and affinities

The outstanding characteristics of *S. arundinaceum* are the large broad leaves; long loose panicle; and the elliptic- to oblong-lanceolate sessile spikelets 6–7·5 mm. long, 2–2·5 mm. wide, awnless or with only short awns 5–10 mm. long. It is closely related to *S. machrochaeta*, from which it is distinguished by the narrower sessile spikelets without awns or with only short awns. The short-awned or awnless sessile spikelets, wider leaves, together with the usually larger panicles, serve to separate it from *S. verticilliflorum.*

Distribution and utility

The natural distribution of this species appears to be mainly in low-lying lands along the Upper and Lower Guinea Coast of West Africa from Sierra Leone southwards to Damaraland. In the Belgian Congo, however, specimens have been recorded as far eastwards as Kindu in Costermansville district. Specimens from East and South Africa previously referred to *S. arundinaceum* probably belong to *S. verticilliflorum.* At an early date during the time of the Slave Trade, probably towards the end of the eighteenth century, *S. arundinaceum* was introduced into some parts of the New World, notably Cuba and Brazil, possible along with the grain Sorghums brought over for food by the negroes of the Guinea Coast of Africa. Although Hackel (in *DC., Monogr. Phan.* **6**, 503, 1889) states that this species, which he names var. *effusus*, is cultivated in Brazil, Piper (in *Proc. Biol. Soc. Wash.* **28**, 37, 1915) thinks that this statement may have been based on information from a herbarium label, and mentions that Dorsett found it as a spontaneous weed, only rarely cultivated. Piper also mentions that at the time his account of the Sorghums was written (1915) it was being tested under cultivation in the



Sorghum arundinaceum (Desv.) Stapf. A, sessile spikelet; B, lower glume; C, upper glume, exterior view; D, lower lemma; E, upper lemma; F, palea; G, grain surmounted by remains of styles. A, ×5; B–G, ×10. (From *Barter* 1379—an awnless form.)

Gulf States of America. It has since spread to other parts of tropical and subtropical America. Although not extensively cultivated for fodder, its strong culms and abundant foliage make it well-suited for that purpose in hot humid regions where species from the drier mountainous regions of Africa are less likely to succeed. *S. arundinaceum* freely inter-crosses with the grain Sorghums of the subseries *Guineënsia* and *Drummondii*, and it seems probable that it has played an important role in the evolution of the West African grain Sorghums from the primitive types.

Specimens of this species are often found in cultivated lands, especially among crops of grain Sorghums, where it is said to become a troublesome weed. It seems to be most common on alluvial soils near streams, usually at lower altitudes up to about 500 m. above sea-level, generally in districts where the climate is hot and humid during the growing season.

VARIETIES

Hackel (in *DC.*, *Monogr. Phan.* **6**, 503, 1889) described two subvarieties of var. *effusus*, namely subvar. *aristatus* with an awn 7–9 mm. long; and subvar. *submuticus* with the awn reduced to a more or less hidden mucro; but in other respects these subvarieties were similar. As the length of the awn is a variable character in some species, and it often varies by as much as 5–10 mm., in the absence of any other correlated character it seems best to regard these subvarieties as variable forms. In his citation of the specimens under *S. arundinaceum* Stapf gave no indication as to those having awned spikelets, but in all those given below that I have seen in the Kew Herbarium the specimens having sessile spikelets with a well-defined kneed or bent awn are denoted by an * immediately after the name or number of the collector.

CANARY ISLANDS. S. Domingos, among sugar cane (Jan. 1860) *Lowe*!

FRENCH GUINEA. A specimen from Baffing Valley, *Pobéquin* 1807, which I have not seen, is cited by Stapf.

SIERRA LEONE. Musaia and Kennema, *Thomas* 2637 *! 7714! Musaia, *Glenville* 317 *! Segbwema, *Deighton* 3473!

Vern. names. Gawonge, Kete, Ndogbo-getei (Mende); Kende, Taiski (La.); Kitanbe, Tokboi (T.); Hula Marutuna, Muruntuna (Yalunka).

LIBERIA. Gbanga, in wet swale, *Linder* 508!

IVORY COAST. Area of Basulé South, between Zoumodi and Kzaakro, *Chevalier* 22,424!

GOLD COAST. Northern Territories, Yapei, riverbank, *Lloyd Williams* 844! Aburi, *Johnson* 799! Winnebah Plains, *Dalziel* 8423! Banks of R. Dansu, at Nsawam, *Irvine* 1938! Without precise locality, *Irvine* 2673 *! Dodowa, *Deighton* 3389! Odumase, *Howes* 1203 *! Without precise locality, coll. *Bunting*, *Howes* 1211! Grown from seed collected by *Vinall*, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 03, 340!

TOGO. A specimen is cited by Stapf from Misahöhe, *Baumann* 151.

NIGERIA. Northern Nigeria: Nupe, *Barter* 1379! Southern Nigeria: Nun River, *Vogel* 50! Lagos, *Dalziel* 1322! Ibadan, *West* *! Ibadan Div., at Oke Ado, *Onochie* 7940 *! Abeokuta province, Egba Div. near Eriwa Road Station, *Onochie* 8143!

Vern. names: Oka-Iye (Yoruba).

CAMEROONS. Victoria—Buea Road, 122 m. *Maitland* 977!

The following specimens are cited by Stapf: Ossidinge, *Mansfield* 8; Mau Tschufi, *Ledermann* 4180; but I have not seen them.

FERNANDO PO. Without precise locality, *Mann* 114!

GUINEA. Without precise locality, *Herb. Willdenow* 18,639 *!

ST THOMAS ISLAND. *Moller* 150 *!

SPANISH GUINEA. Nkolentangan, Aleu, *Tessmann* 257 *!

A specimen from Fan, *Tessmann* 93, is cited by Stapf.

GABOON. Adolinalongo, *Soyaux* 284!

BELGIAN CONGO. Stanley Pool, *Vanderyst* 3943 *! Barumba, *Bequaert* 1180! Costermansville, near River Congo, Kindu, *Shantz* 607 *! 623! 624! Kibwamba, *Shantz* 610! Kiti (1910), *Flamigni* 374! Kitobola, (1920), *Flamigni* 204! Butir and Buta, *Robyns* 1226!

The following specimens are cited by Stapf which I have not seen: Kisantu, *Gillet*; Lower Congo, *Smith*; without precise locality, *Demeuse*.

ANGOLA. I have not seen any specimens from this country, but Stapf cites the following: Cazengo, at Caculo, *Welwitsch* 2994; Ambriz, *Welwitsch* 2898; 2898/3; Icolo and Bengo, by the Bango River, *Welwitsch* 7197.

DAMARALAND. Stapf cites the following specimens which I have not seen: Tsoachaub, *Fleck* 403; Kuisib, *Fleck* 469; without precise locality, *Een*.

BRAZIL. Paraiba: ex Herb. Rep. Berolinense, *Sellow* 1250 *! Sergipe Sao Christovao, *Mun* 3745 *! Bahia: ex Herb. Hook. (1867), *Saltyman*! Minas Gerais: *Saint Hilaire* (Catal. 'A', 524) M. 339 *! on the ascent to Bovcorado (Bocauiva?) *Gardner* 144 *! Rio de Janeiro: comm. *Glaziou* (*Guinta* 31) 3150 *! 1633 *! 6961 *! *MacGillivray* 212 *! ex Herb. Hort. Petropolitani, *Reidel* 1231 *! Without precise locality *Burchell*, 1632 *!

A specimen from Pernambuco, ex Herb. Hook., 1867 (common in waste and cultivated places, No. 1837), *Gardner* 1177! may be a weak immature flowering state of this species.

Besides the synonyms already given above, Hackel included under *Andropogon sorghum* var. *effusus* the names *Holcus decolorans* Willd., *Sp. Pl.* **4**, 931, 1805; *Andropogon decolorans* Kunth in Humbolt et Bonplond, *Nov. Gen.* **1**, 190, 1815; and *Sorghum decolorans* Roem. et Schult., *Syst. Veg.* 2, 838, 1817 (the two latter being new names for *Holcus decolorans* on transferring the species to different genera). He also included *Trachypogon avenaceus* Nees in Martius, *Fl. Bras.* **2**, 354, 1829, which is a different generic reference for *Andropogon avenaceus* Kunth (loc. cit. p. 189), and may have been inadvertently used instead of *A. arundinaceus*; as well as *Sorghum halepense* Nees, *Fl. austr.* p. 88, 1841 [non *S. halepense* (Linn.) Pers., *Syn.*, **1**, 101, 1805].

Holcus decolorans Willd. and *Andropogon decolorans* Kunth were based on specimens from Cuba and Venezuela. As all the specimens from those countries at that time in the United States National herbarium were *Andropogon halepense* (Linn.) Brot., a species with perennial rhizomes, Piper (in *Proc. Biol. Soc. Wash.* **28**, 35, 36, 1915) considers the above references doubtful, except those concerning the inadvertent use of the name *Trachypogon avenaceus* Nees, which had particular reference to specimens from Brazil, where var. *effusus* (*Andropogon arundinaceus*) is abundant. Regarding *Sorghum halepense* Nees (non Pers.), no special reference is made by Piper, but it was later included by Stapf (in Prain, *Fl. Trop. Afr.* **9**, 117, 1917) in synonymy under *S. verticilliflorum*, to which these South African specimens belong.

I have been able to examine only a few of the specimens cited by Hackel under var. *effusus*, but it is evident that he included elements of more than one species, as since recognized by Piper, Stapf, and myself. The first specimen cited by Hackel, *Schweinfurth* 1521, from the Anglo-Egyptian Sudan, is the type of *S. macrochaeta*, and that of *Böhm*, from Lake Tanganyika, belongs to the same species; those of *Moller* and *Barter*, from West Africa, are both *S. arundinaceum*; that of *Drège* from South Africa is *S. verticilliflorum*. The other specimens from Natal, Mauritius, and Madagascar, cited by Hackel, have not been seen by me but probably belong either to *S. verticilliflorum* or a related East African species.

11. **Sorghum verticilliflorum** (Steud.) Stapf

Andropogon verticilliflorus Steud., *Syn. Pl. Glum.* **1**, 393, 1854, was founded on a specimen from the island of Bourbon (Réunion).

A. sorghum (Linn.) Brot. subsp. *verticilliflorus* Piper in *Proc. Biol. Soc. Wash.* **28**, 37, 1915, is based on Steudel's species.

Holcus sorghum Linn. subsp. *verticilliflorum* (Steud.) Hitchc. in *Proc. Biol. Soc. Wash.* **29**, 128, 1916, has the same basis.

Sorghum verticilliflorum (Steud.) Stapf in Prain, *Fl. Trop. Afr.* 9, 116, 1917, is also based on *Andropogon verticilliflorus* Steud.

I have not been able to see, or to locate, the type specimen, but after careful examination of all the Sorghum material from East and South Africa available at Kew, including specimens from Bourbon and the neighbouring islands collected soon after Steudel's description was published, I find that some of the material from the East African coastal area and the islands in the Indian Ocean differ from *Sorghum verticilliflorum* (as described by Stapf and since generally accepted), and is best treated as a related but distinct species which I have named *S. brevicarinatum* (see no. 14).

Description

An annual or loosely tufted perennial 1–3·5 m. high. *Culms* slender to somewhat stout, 5–10 mm. wide, sometimes purplish below the nodes. *Leaves* few to many; blades linear, with a rather broad rounded base, tapering gradually upwards to the pointed apex, about 30–60 cm. long, 1–3 cm. wide, green, sometimes glaucous, often flushed with purple, with the paler stoutish mid rib gradually narrowing upwards. *Panicle* 15–50 cm. long, 5–15 cm. wide, pyramidal to ovate-elliptic or elliptic-oblong, somewhat contracted or more often loose and spreading; branches slender, ascending or at length flexuous and bending outwards, shortly hairy to somewhat villous at the base, the lower ones often 3–5 in a whorl and 5–20 cm. long, sparingly branched and usually bare of spikelets for 2–5 cm. from the base. *Racemes* fragile, 2- to 5-noded, 1·5–2·5 cm. long; internodes and pedicels slender, 2·5–4 mm. long, densely ciliate with greyish white, tawny or purplish hairs. *Sessile spikelets* elliptic-lanceolate, acuminate, mostly 6–7 mm. long (but sometimes reduced to 5·5 mm.), 2–2·5 mm. wide, with 5–7 nerves evident between the keels of the lower glume, pale yellow to deep cream, or at length becoming reddish brown to purplish or black, usually more or less strigosely hairy when young but often glabrous and shining on the exposed portions when mature; awned; callus beard scanty to copious. *Glumes* coriaceous for the most part but somewhat thinner in the upper third where the nerves become visible; lower rather flat above the middle, with 11–13 primary nerves, some cross-nerves above the basal third, 2-keeled from just above the middle, with the spinulously ciliolate keels narrowly margined and terminating in obscure or very minute teeth below the hyaline tip; upper with 7 (rarely 8) primary nerves, cross-nerves present in the upper half, keeled above the middle, more sharply in the upper fourth where it is more or less rough. *Lemmas* densely long-ciliate; lower elliptic-lanceolate, 4·5–6 mm. long; upper ovate to ovate-elliptic, 3–5 mm. long, 2-lobed to 1·5 mm. deep, awn 10–16 (rarely 18) mm. long. *Anthers* 2·5–4 mm. long. *Grains* obovate-elliptic to obovate, 2·5–3·5 mm. long, 1·5–2 mm. wide, pale to dark brown or dark red, embryo-mark distinct. *Pedicelled spikelets* ♂ or sometimes reduced, deciduous, pale greenish yellow or often reddish to purplish, 5–7 mm. long; lower glume 8- to 10-nerved, upper 5- to 6-nerved; anthers 2·5 mm. long.

Diagnostic characters and affinities

The slender to somewhat stout culms; long narrow leaves mostly 0·5–2·5 cm. wide; and narrow elliptic-lanceolate, rather long-awned sessile spikelets, usually 6–7 but sometimes 5·5 mm. long, are the distinguishing features of *S. verticilliflorum*. The narrow leaves serve to separate it from both *S. arundinaceum* and *S. macrochaeta*. It also has longer awns than the former and narrower somewhat shorter-awned spikelets than the latter. In normal well-developed specimens of *S. arundinaceum* and *S. macrochaeta* the panicles are usually larger than those of *S. verticilliflorum*, but this difference is not always apparent as the size of the panicles is apt to vary somewhat according to the conditions under which the plants have been grown. *S. brevicarinatum* differs in the ovate-elliptic sessile spikelets, 4·5–5·5 mm. long, with shorter broader-margined keels, and leaves often 3–5 cm. wide. The shape of the lanceolate sessile spikelets distinguishes *S. lanceolatum* from *S. verticilliflorum*.

DISTRIBUTION AND UTILITY

In North Africa the natural distribution of this species commences near the northern boundaries of Uganda and Kenya, but it also occurs in southern Abyssinia and Italian Somaliland. Southwards it extends through Tanganyika Territory, Nyasaland and Rhodesia to South Africa as far as the Orange River and Natal. Its western limit is generally near the borders of the western Rift Valley (including that part of the Belgian Congo which adjoins it) until it reaches Northern Rhodesia, but a single specimen has been recorded from Benguella, Angola, on the West African coast. On the east it does not appear to be common in the coastal lands of Kenya and Tanganyika Territory, but it has been recorded from near the mouth of the Zambesi River, as well as from the Mascarene Islands, including Réunion (Bourbon). It seems probable that it originated somewhere in the vicinity of the Great Lakes and Upper Nile region of Central Africa, where it is most abundant and widespread, but was carried southwards along the lakes and rivers of the western and eastern Rift Valleys by the Bantu races as they travelled southwards to the Transvaal, Orange Free State, and Natal, whence it was introduced into some of the Islands of the Indian Ocean. During more recent times it has been introduced into various countries, including India, Australia, Polynesia, and the West Indies.

Many of the African native races look upon it as a wild state of their cultivated grain Sorghums, and in times of famine the natives sometimes eat the grains from the wild plants. It intercrosses freely with the Sorghums cultivated in areas where it grows wild, especially varieties of *S. roxburghii*, *S. caudatum*, and *S. caffrorum*, and specimens that have evidently resulted from such cross-fertilization are often encountered. It has been cultivated to some extent as fodder, in those stock-raising countries into which it has been introduced, including some parts of South Africa and Australia. For this purpose it has about the same utility as Sudan Grass (*S. sudanense*), but it is doubtful if it will entirely replace the latter species, as it suffers from the disadvantage of the fragile racemes shattering when mature, which makes the collection of seed more costly and difficult.

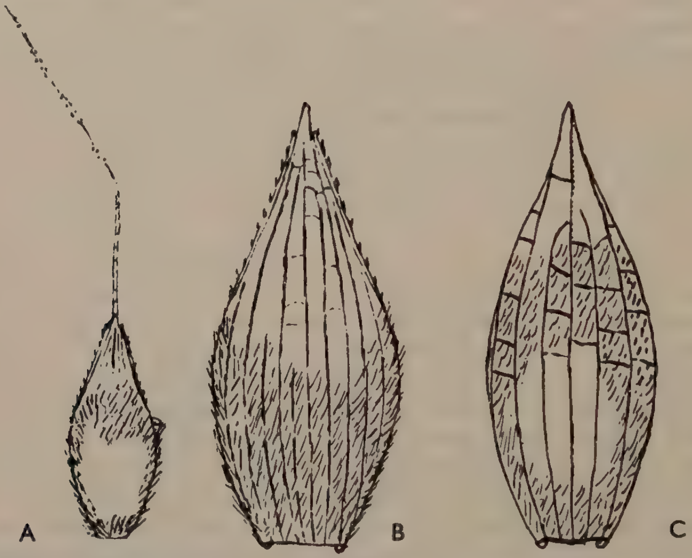
The toxicity of *S. verticilliflorum* is about equal to that of *S. sudanense*, and cases of Sorghum poisoning due to animals feeding on it have been reported from South Africa and Australia. In Steyn's account of 'The Toxicology of Plants in South Africa' (*Onderstepoort J. Vet. Sci.* **3**, 421–2, 1934), under the heading *S. verticilliflorum*, on p. 421, the South African Sorghum concerned is probably this species, but there is also much reference to Johnson Grass (*S. halepense* Pers.), which has wide-spreading rhizomes and should be easily distinguishable from *S. verticilliflorum*. In Australia, in *The Poison Plants of New South Wales*, p. 28, 1942, Hurst records under *S. verticilliflorum* that White states the HCN content of this species to be exceedingly high at practically all stages of growth and that in this respect it is one of the worst Sorghums so far tested. It is said to be dangerous to stock almost throughout the growing period and strongly cyanogenetic. The use of this species as fodder for domestic animals would therefore appear to need careful investigation and control, although under normal conditions most Sorghums generally become harmless at maturity.

S. verticilliflorum is generally found growing in or near to cultivated lands, especially in abandoned cultivations that are overgrown and reverting to a mixture of grassland, bushland and woodland. Though often found near lakes and streams, it is probably still more frequent on hilly lands. The variety *infrequens* has a limited distribution and is found mainly in areas near the equatorial region of Africa, but var. *ornatum*, which appears to be the most common, and var. *verticilliflorum* extend from the northern to the southern limits of distribution in Africa. The former is generally most frequent on the reddish soils of the hill lands and the latter is more often found on the dark soils of the plains and valleys, but the factors governing their local appearance are by no means clear. Var. *verticilliflorum* is the one generally found in India and Australia.

(i) Var. **verticilliflorum**

Var. **verticilliflorum** is based on *Andropogon verticilliflorus* Steud. I have not yet been able to locate the type specimen of the species, but the variety, as here defined, is restricted to those plants with rather broad and somewhat short sessile spikelets.

Sessile spikelets broadly elliptic-lanceolate, 6–6·5 mm. long, 2–2·5 mm. wide, mostly dull cream to tawny, but sometimes reddish to black; base of the lower glume rather wide and somewhat pear-shaped.



Sorghum verticilliflorum (Steud.) Stapf var. *verticilliflorum*. A, sessile spikelet and apex of pedicel; B, lower glume; C, upper glume, exterior view. A, ×5; B and C, ×10. (From *Balfour*, coll. on Bourbon Island.)

Belgian Congo. Mahagi Port, near Lake Albert, 625 m., *Johnson* 1153! Bunia, near Lake Albert, 1370 m., *Johnson* 1109! Semliki Valley, 670 m., *Johnson* 1223! Bukama, on river bank, *Shantz* 561! Francis Camp, west of Lake Uionga, *Shantz* 589! Msala, near Nyanza, Lake Tanganyika, *Shantz* 679!

Uganda. Teso district, Serere, 1097 m., *Chandler* 743! Bulemezi, *Johnson* 102! Plains of Lake Albert, near Butiaba, 610 m., *Johnson* 942! Toro district, at Kikorongo, 1087 m., *Maitland* 1400!

Vern. name: Muhembahemba (Luganda).

A specimen collected near Lake Kioga, *Michelmore* 1212! is somewhat intermediate between this variety and *S. niloticum*. It may have resulted from intercrossing between one of these two species and a cultivated grain Sorghum.

Kenya Colony. Kavirondo country, 6 days' march from Mumias (1898), *White*! Nyanza province, Maseno, 1524 m., *Benstead* 3101! South Kavirondo, Kitutu, 1676 m., *Spranger* S62! Machakos district, Kibwezi, 884 m., *Dummer* 4544! Lorgasailie Plains, 1158 m., *Andrews* B5190!

Vern. name: Hesamu.

TANGANYIKA TERRITORY. Moshi district, 915 m., *Haarer* 364! Mpwapwa district, *Staples* 251!

NORTHERN RHODESIA. Chilonga district, at Quien Sabe and Kusaka Farm, *Sandwith* 20! 62!

SOUTHERN RHODESIA. Makwiro district, *Mainwaring* 7640! Makwiro, 1310 m., *Eyles* 2100! Salisbury, 1430 m., *Eyles* 2121! ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 56,801!

NYASALAND. Between Kondowe and Karonga (1896), *White*! Port Herald Experiment Station, *Lawrence* 46!

PORTUGUESE EAST AFRICA. Msalu River, Nyasa district, *Allen*! Boruma, *Meynharth* 1044!

MASCARENE ISLANDS. Réunion (Bourbon) Island, *Balfour*!

MAURITIUS. Without precise locality (Oct. 1872), *Pike*! *Vaughan* A8!

A specimen grown from seed collected by *Reed* at Reduit, Mauritius, and cultivated at Chula Vista, California, ex *U.S. Agric. Dep. Sorghum Herb. S.P.I.* 40,897! has wider leaves and persistent spikelets and may be the result of intercrossing between this species and a cultivated grain Sorghum.

SEYCHELLE ISLANDS. Ex *U.S. Agric. Dep. Sorghum Herb. S.P.I.* 40,773!

INDIA. Without precise locality, *Wallich* 8778 D/3! 8778 F/1! *Herb. Wight* 1672! Mirittipadu (Nov. 1794) *Herb. Rottlerianum*!

Vern. name: Tabucki Grass from the Cape (from South Africa).

Specimens from Madras, used in hybridization experiments with *Saccharum* spp., *Janaki Ammal* 1235! may be hybrid forms of this variety.

AUSTRALIA. Queensland: Brisbane, Upper Brookefield near Brisbane, and Brisbane River, *White* (June, 1926)! 6! 11! Brisbane, Kangaroo Point, *Winchester*! Between Pinkinba and Meeandah, near Brisbane, *Blake* 5029! Terongpilly, near Brisbane, *Longman*! Brisbane and vicinity, including Sherwood, Milton, Toowong, and banks of the Brisbane River, *Hubbard* 2378! 2872! 4730! 2167! 4809! Between Lanesfield and Rosewood, 36 miles south-west of Brisbane, *Hubbard* 2142! Emerald, *Hubbard* 7922! Between Teirotville and Anthony, Hubbard 5370! Chudleigh Park Station, 110 miles north of Hughenden, *Hubbard & Winders* 7658! Petrie, *Blake* 228! Pialba, *Pointon*! Booyal via Childers, *Colman* 19! Toowong Creek near One Tree Hill, *Blake & Everist* 222! Port Jackson to Blue Mountains, *Cunningham*! Stratford near Cairns, *Dalziel*! State Farm, Hermitage, Warick, *Liverseed* 8! Waterford, *Mead*!

Cunningham's specimen was cited by Bentham (in *Fl. Aust.* 7, 540, 1878) under *S. plumosum* Beauv.

COOK ISLANDS. Karatonga, *Cheeseman* 723!

SAMOA. Upsolu (May 1895), *Flora Samoensis, Reineke*!

SOLOMON ISLANDS. *White, B.S.I.P.* 132!

SOCIETY ISLANDS. Tahiti, ex *U.S. Agric. Dep. Sorghum Herb. S.P.I.* 42,278!

ST VINCENT. Without precise locality, *Maling* 5! *Guilding* 2822!

ST KITTS. Pond Estate, near Basseterre, *Box* 130!

CUBA. Bayamesa, 500 m., *Fl. Indiae Occidens, Eggers* 4678!

DOMINICAN REPUBLIC. Barahona province, near Rincon, *Flora Domingensis leg. Pedre Miquel Fuertes* (Oct. 1911)!

(ii) Var. **ornatum** Snowden

Var. **ornatum** Snowden, var.nov.; spiculae sessiles anguste elliptico-lanceolatae, 6–7 mm. longae, 2–2·5 mm. latae, saepe rubrae vel purpureae, demum cacao-brunneae, vel nigrae; gluma inferior basin versus angusta, amygdaliforma.

Sessile spikelets narrow elliptic-lanceolate, 6–7 mm. long, 2–2·5 mm. wide, often reddish to purplish coloured, or at length dark chocolate brown to black; base of the lower glume slender, curving gradually outwards and more or less almond-shaped.

This variety is based on two specimens in the Kew Herbarium collected by *Drège* near the Orange River at Verleptpram.

ANGLO-EGYPTIAN SUDAN. Nimule, near the boundary with Uganda, *Shantz* 895! 899!

UGANDA. Karamoja district, Napak, 1220 m., *Thomas* 3657! Mbale district, near Mbale, *Snowden* 1099! Entebbe district, at Entebbe (1902), *Mahon*! Victoria Nyanza Region, 1175 m., *Maitland* 89! 92! Mengo district, at Kipayo, 1220 m., *Dummer* 474! 1278! Masaka district, near Masaka, 1280 m., *Snowden* 1388! Ankole district, near Mbarara, 1402 m., *Snowden* 1374!

Vern. name: Muhembahemba (Luganda).

The specimen *Dummer* 1278 is malformed owing to damage by 'Smut Disease'.

KENYA COLONY. Nyanza province: Maseno, 1524 m., *Sampson* 85! Fort Ternan and Koro, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 51,577! 51,578! Fort Hall district, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 51,439! *Pole Evans* 1168! 16 miles north of Thika, *Pole Evans* 1172! Blue Post, near Nairobi, *Shantz* 834! Embu to Nairobi, *Shantz* 973! Nairobi, *Dowson* 315! Kisii, 1646 m., *Napier* 5368!

TANGANYIKA TERRITORY. Moshi district, Marangu, *Davis* 1129! Pare district, Kiruru, 762 m., *Haarer* 1280! Kondoa district, near Sambala, 1463 m., *Burtt* 2605! 18 miles north of Mawhamuta, *Pole Evans* 1009! Central Railway at Lyamungu, 1310 m., *Wallace* 1161! Kasunika, near Rungwa, *Michelmore* A.C. 1603! without precise locality, *Rounce* 330!

Vern. name: Sambankona (Chi-Fipa).

NORTHERN RHODESIA. Lunsefwa River, *Burtt Davy* 904/29!

SOUTHERN RHODESIA. Salisbury: *Townsend* (Feb. 1909)! Makwiro district, ex *Dep. Agric. Herb.* 42 (27/21)!

NYASALAND. Near Chiromo, 38 m., *Wiehe* 207!

PORTUGUESE EAST AFRICA. Below Mazzawo, between Tette and the sea, *Kirk* (March–April, 1860)!

BECHUANALAND. Banks of the Zebanini River, *Pole Evans* 3319(15)!

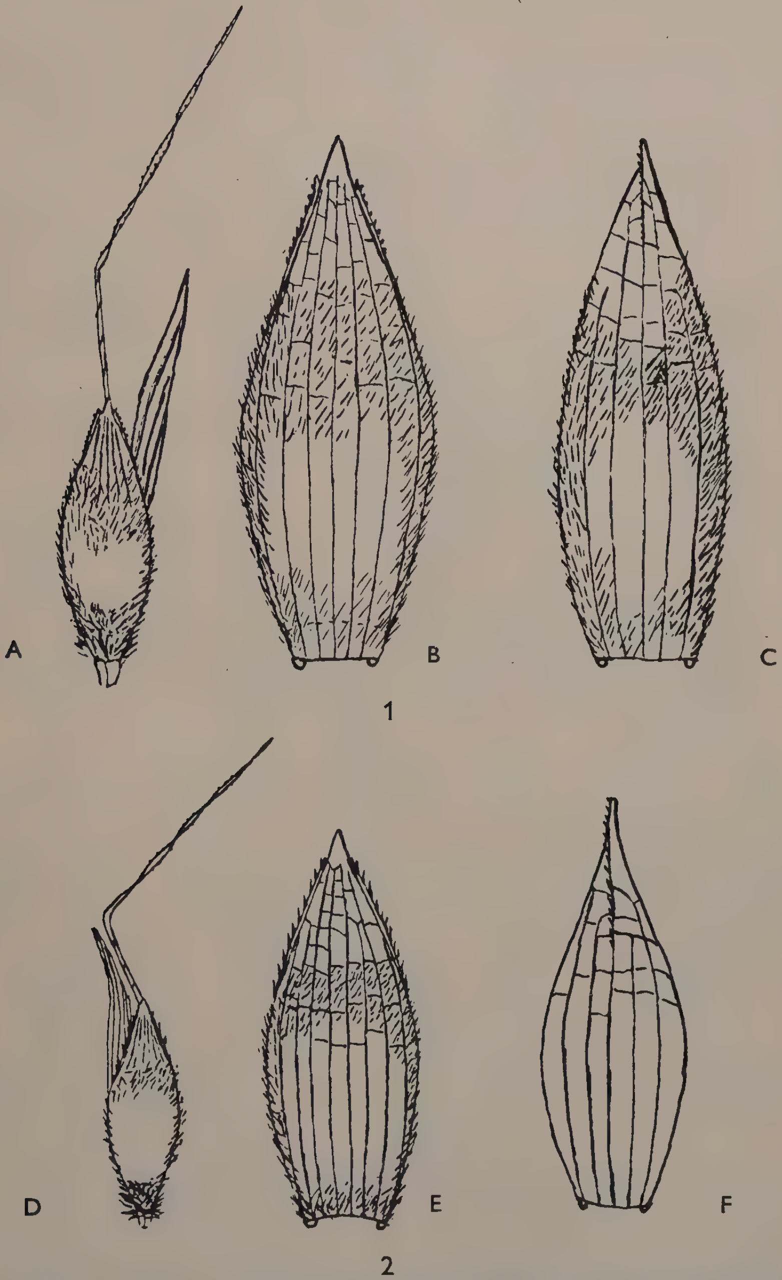
SOUTH AFRICA. Cape province: Hereroland, at Tsavehaub and Kuisib, *Fleck* 403! 469! Little Namaqualand, at Verleptpram near the Orange River, below 150 m. (Sept. 1840), *Drège*! Pondoland, Tamvoona River, *Burtt Davy* 15,373! Herbert district, St Clair near Douglas, 1050 m., *MacOwan* 185! 1995! Knysna Division, on the hills near Melville, *Burchell* 5465B! Upington, on the banks of the Orange River, *Moss* 10,980! Kimberley, from seed obtained near the Vaal River, *Wilman* C7! Natal province: Durban, *Gerrard* 690! Verulam, *Rehmann* 9070! Umhlanga, *Wood* 1332! near the Umlazi River, *Krauss* 184! Banks of the Tugela River, *Buchanan* 296! Transvaal province: Pretoria, cultivated but indigenous, *Melle* H20, 940! Seed from Pretoria and Nelspruit, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 40,832! 49,304!

Another specimen from *U.S. Sorghum Herb., S.P.I.* 38,866! which has wider leaves and tough racemes, is probably the result of intercrossing with a cultivated race.

(iii) Var. **infrequens** Snowden

Var. **infrequens** Snowden, var.nov.; spiculae sessiles anguste elliptico-lanceolatae, 5·5–6 mm. longae, 2–2·2 mm. latae, plerumque rubrae, rubido-brunneae, vel nigrae, pilis rubiginosis vel rubidopurpureis saepe dense strigosae, raro pilis subalbidis et glabrescentes; gluma inferior basin versus angusta, amygdaliforma.

Sessile spikelets narrow elliptic-lanceolate, 5·5–6 mm. long, 2–2·2 mm. wide, mostly mahogany-red to reddish brown or black, usually densely strigose with ferruginous to reddish purple hairs, but sometimes almost glabrous with the hairs whitish; base of the lower glume slender, curving gradually outwards and more or less almond-shaped.



Sorghum verticilliflorum (Steud.) Stapf. (1) Var. *ornatum* Snowden. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view. (From *Drège*, coll. by the Orange River.) (2) Var. *infrequens* Snowden. D, sessile and pedicelled spikelets; E, lower glume; F, upper glume, exterior view. (From *Thomas* 3884.) A and D, × 5; B, C, E and F, × 10.

The type of this variety is a specimen collected at Athobi, in the Lango district of Uganda, *Thomas* 3884, in Kew Herbarium.

ABYSSINIA. Modjo, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 58,742!

UGANDA. Lango district, at Athobi, 1070 m., *Thomas* 3884!

KENYA COLONY. Fort Hall, near Nairobi, *Shantz* 835! Blue Post to Nairobi, *Shantz* 836! Embu to Nairobi, *Shantz* 976! 977! 979! Meru and Thika, ex *U.S. Dep. Agric. Sorghum Herb. F.C.I.* 8678! 8698!

TANGANYIKA TERRITORY. Kigoma, near Lake Tanganyika, *Shantz* 764!

ANGOLA. Near Port Amboin, *Gossweiler* 9770!

BRITISH GUIANA. New Amsterdam, *Hitchcock* 16,818!

Nees von Esenbeck (in *Fl. Afr. Aust.* p. 88, 1841) placed the South African Sorghums under *Sorghum halepense*, which is a perennial with well-developed rhizomes having a natural distribution more or less confined to the Mediterranean Region and the adjacent parts of western Asia. Up to that time, however, most of the wild Sorghums had been regarded as varieties of *S. halepense*, so that it is easy to understand why they were referred to the latter species. Unfortunately it has since led to some confusion on account of *S. halepense* having been placed by many authors in the synonymy of other species and varieties of *Sorghum* that do not possess distinct rhizomes and have since been separated into a different subsection, *Arundinacea*.

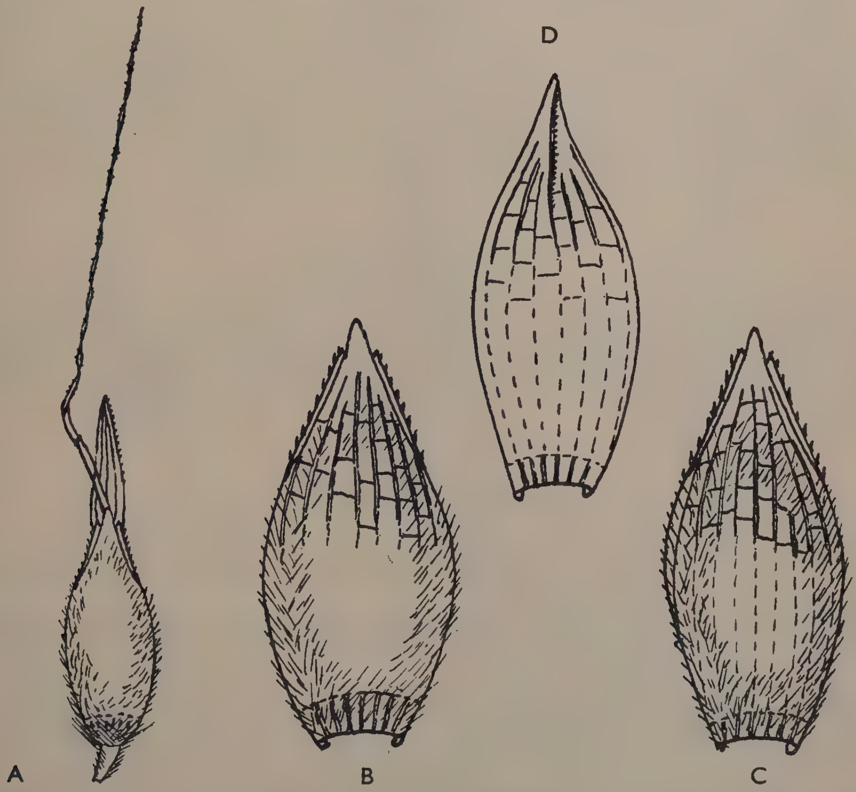
Hackel (in *DC.*, *Monogr. Phan.* **6**, 503, 1889) included these South African Sorghums under *Andropogon sorghum* var. *effusus*, which as here understood is restricted to *Sorghum arundinaceum* (Willd.) Stapf, (in Prain, *Fl. Trop. Afr.* **9**, 114, 1917), based on *Andropogon arundinaceus* Willd. Before this revision of the African Sorghums was completed Stapf, when dealing with the Sorghums in Hook., *Fl. Brit. India*, **7**, 183, 1896, and in Dyer, *Fl. Cap.* **7**, 346, 1898, had not fully defined the limits of the genus *Andropogon* and therefore had no alternative but to follow Hackel in placing the wild species of Indian and South African Arundinaceous Sorghums under *A. halepensis* (Linn.) Brot.

12. **Sorghum somaliense** Snowden

Sorghum somaliense Snowden, sp.nov.; affine *S. verticillifloro* (Steud.) Stapf sed culmis gracilioribus, humilioribus, foliis parvioribus, laminis foliorum apicibus longe attenuatis filiformibus, panicula parviore angustiore, spiculis sessilibus elliptico-lanceolatis vel ellipticis acutis, 5·5–6 mm. longis, aristis longioribus gracilioribus differt.

Gramen annuum, 0·5–1 mm. altum. *Culmi* graciliusculi, basin versus 3–4 mm. lati. *Folia* pauca, laminae anguste lineari-lanceolatae, 10–30 cm. longae, 0·5–2 cm. latae, basi latiusculae vel leviter contractae, in apicem filiformem longe attenuatae, costa media validiuscula subalbida. *Panicula* anguste oblonga, 10–25 cm. longa, circiter 1–2 cm. lata, laxa; axis primarius sursum angulatus, striatus, scabridus; rami solitari vel 2–3-nati, gracillimi, erecti vel suberecti, superne tenuiter spinulose ciliati, basin versus leviter hirsuti, inferiores 3–8 cm. longi, saepe 1–2 cm. nudati. *Racemi* fragillimi, 2–5-nodis, 1–2·5 cm. longi; rhacheos internodia gracillima, 2–3 mm. longa, pilis subalbidis vel pallido-purpureis 0·5–1 mm. longis ciliata; pedicelli internodiis similes. *Spiculae sessiles* elliptico-lanceolatae vel ellipticae, acutae, 5·5–6 mm. longae, 2–2·5 mm. latae, aristatae, primo stramineo-flavae vel eburneo-flavae plus minusve hirsutae, vel demum saepe pallido- vel atro-purpurascentes, dorsis glumarum fere glabrae; callus dense barbatus. *Glumae*, regione apicali tenui et chartacea excepta, coriaceae; inferior 12-nervis, triente superiore bicarinata, carinis spinulose ciliolatis, dentibus minutis nonnunquam terminatis; superior 7-nervis, apicem versus carinata, carina scabrida. *Lemmata* tenuiter longiciliata; inferius elliptico-oblongum, 4·5–5 mm. longum, exiliter 2–3-nerve, apice breviter bidentatum incisione circiter 0·3 mm. diametro paene orbiculata; superius elliptico-ovatum, 2·5–4 mm. longum, tenuiter 3-nerve, breviter bilobum, arista gracilis, 15–18 mm. longa. *Antherae* 2 mm. longae. *Caryopsides* ellipticae, circiter 3·5 mm. longae, 2 mm. latae, nigro-brunneae. *Spiculae pedicellatae* lineari-lanceolatae, acuminatae, 5–6 mm. longae, ♂ vel interdum redactae, stramineo-flavae vel virido-flavae, deciduae; gluma inferior 8–9-, superior 5-, nervis; antherae 1·5–2 mm. longae.

An annual 0·5–1 m. high. *Culms* rather slender, about 3–4 mm. wide near the base. *Leaves* few; blades narrowly linear-lanceolate, 10–30 cm. long, 0·5–2 cm. wide, with a rather broad or slightly contracted base, long-tapering upwards into a filiform tip, with the mid rib rather stout and whitish. *Panicle* narrow-oblong, 10–25 cm. long, about 1–2 cm. wide, loose; rhachis angular, striate and rough in the upper part; branches solitary or 2- to 3-nate, very slender, erect or suberect, finely spinulously ciliolate upwards, slightly hairy near the base, the lower 3–8 cm. long, often bare for 1–2 cm. from the base. *Racemes* very fragile, 2- to 5-noded, 1–2·5 cm. long, internodes and pedicels slender, 2–3 mm. long, ciliate with whitish or pale-purplish hairs 0·5–1 mm. long. *Sessile spikelets* elliptic-lanceolate to elliptic, acute, 5·5–6 mm. long, 2–2·5 mm. wide, pale straw to cream colour with greenish nerves evident near the tip of the lower glume when young, at length light to dark purple, coarsely hairy with whitish hairs or glabrescent on the backs of the glumes, awned; callus densely bearded. *Glumes* coriaceous for the most part but somewhat thinner near the tip; lower 12-nerved, with a few cross-nerves above the middle, 2-keeled in the upper third with the spinulously ciliolate keels sometimes ending in minute teeth; upper 7-nerved, with a few fine cross-nerves in the upper half, keeled towards the tip, scabrid on the keel. *Lemmas* finely long-ciliate; lower elliptic-oblong, 4·5–5 mm. long, finely 2- to 3-nerved, the 2-toothed apex with an almost circular



Sorghum somaliense Snowden. A, sessile and pedicelled spikelets; B, lower glume of fruiting spikelet; C, lower glume of younger spikelet; D, upper glume; all three exterior view. A, × 5; B–D, × 10. (From *McKinnon* S/274.)

notch about 0·3 mm. in diameter; upper ovate-elliptic, 2·5–4 mm. long, faintly 3-nerved, 2-lobed to 0·5–0·7 mm. deep, with a slender awn 15–18 mm. long. *Anthers* 2 mm. long. *Grains* elliptic, about 3·5 mm. long and 2 mm. wide, dark brown. *Pedicelled spikelets* linear-lanceolate, 5–6 mm. long, ♂ or sometimes reduced, straw-yellow or somewhat greenish, deciduous; lower glume 8- to 9-nerved, upper 5-nerved; anthers 1·5–2 mm. long.

The type of this species is a specimen in Kew Herbarium, *McKinnon* S/274, collected in Somaliland.

Diagnostic characters and affinities

S. somaliense is related to *S. verticilliflorum* Stapf but differs in the more slender shorter culms; smaller leaves with long-tapering filiform tips; the smaller, narrower and sparsely branched panicle; and in the sessile spikelets elliptic-lanceolate to elliptic, acute, 5·5–6 mm. long, 2–2·5 mm. wide, with longer more slender awns. The small narrow leaves with filiform tips, the sparse panicle with the branches keeping close to the main axis, together with the almost elliptic sessile spikelets with comparatively long slender awns, form the most characteristic features of this species.

Distribution and utility

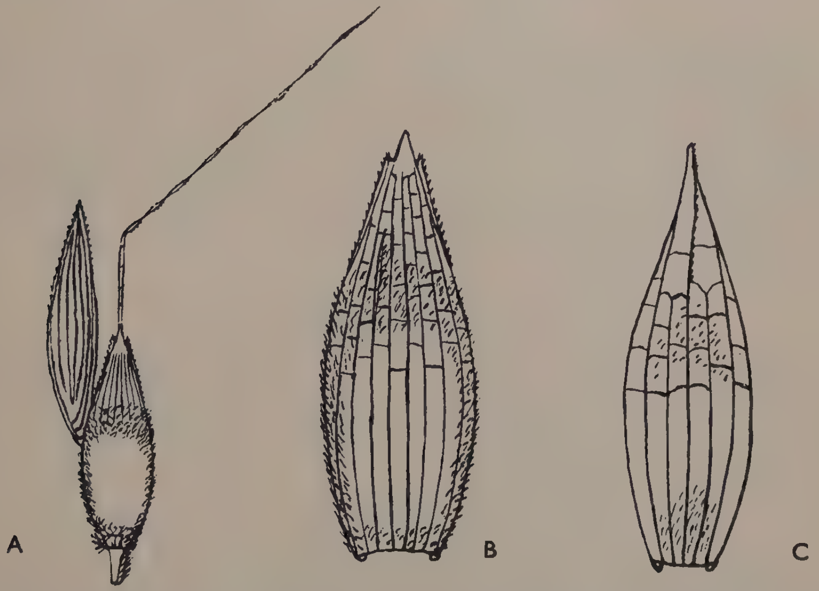
The original gathering from Somaliland is the only material of this species that has been received at Kew. No information is at present available as to its utility. The foliage is not luxuriant enough to suggest a very good fodder plant. It appears to have been grown in a very dry region, however, and it might prove useful in districts with a low rainfall and a hot climate.

13. **Sorghum pugionifolium** Snowden

Sorghum pugionifolium Snowden, sp.nov.; a *S. somaliensi* Snowden culmis gracilioribus, foliis parvioribus saepe pugioniformis, spiculis sessilibus oblongo-lanceolatis acuminatis, glumis subcoriaceis differt.

Gramen annuum, 50–60 cm. altum. *Culmi* graciles, 1–2 mm. lati, plerumque simplices. *Folia* pauca; vaginae superiores plerumque ter, quater, vel quinquies longiores quam laminae; ligulae superiores subdeltoides, 2–3 mm. longae; laminae saepe pugioniformae, angustae, longi-acuminatae, 4–10 cm. longae, 3–9 mm. latae, glabrae, nervo medio gracile pallidiore excepto, virides. *Panicula* anguste oblonga, 4–12 cm. longa, 1–2 cm. lata, e vagina summa 8–12 cm. exserta; axis primarius gracilis, teres, tenuiter striatus; rami graciles, 1–3-nati, 1–7 cm. longi, superne tenuiter spinulose ciliolati, basin versus hirsuti 1–2 cm. nudati, cetera glabri. *Racemi* fragiles, 2–4-nodis, 1–1·5 cm. longi; rhacheos internodia gracillima, 2·5–4 mm. longa, saepe purpurascentia, pilis subalbidis 0·5–1 mm. longis ciliata; pedicelli internodiis similes. *Spiculae sessiles* oblongo-lanceolatae, acuminatae, 5·5–6·5 mm. longae, 1·5–2 mm. latae, aristatae, stramineo-flavae, flavae, vel purpureae, pilis subalbidis vel fulvis sparse hirsutae vel dorso glumarum glabrescentes; callus breviter barbatus. *Glumae* subcoriaceae; inferior 12–13-nervis (prope apicem 3–5-nervis apertis), supra medium tenuiter bicarinata, carinis spinulose ciliolatis dentibus minutis vel obscuris terminatis; superior 7-nervis, triente superiore tenuiter carinata, carina scabrida. *Lemmata* moderate ciliata; inferius elliptico-lanceolatum, 5·5 mm. longum, 2-nerve; superius ovatum, 3·5–4 mm. longum, 1–3-nerve, breviter bilobum, arista 12–14 mm. longa praeditum. *Antherae* 3·5 mm. longae. *Caryopsides* (immature) ellipticae, 1·5 mm. longae. *Spiculae pedicellatae* lineari-lanceolatae vel subulatae, plerumque ♂, 6–7 mm. longae, deciduae; gluma inferior 9–12-nervis; gluma superior 6–7-nervis; antherae 3–3·5 mm. longae.

A loosely tufted annual, 50–60 cm. high. *Culms* slender, 1–2 mm. wide, usually simple. *Leaves* few; uppermost sheaths usually clasping the culms and 3–5 times as long as the blades, somewhat pubescent near the nodes and the junction with the blades; ligules membranous, subdeltoid, 2–3 mm. long, hairy at the base; blades narrow, often dagger-shaped, long-acuminate, 4–10 cm. long, 3–9 mm. wide, glabrous, greenish, with a slender paler mid rib. *Panicle* narrow-oblong, 4–12 cm. long, 1–2 cm. wide, long-exserted (8–12 cm.) from the uppermost leaf-sheath; rhachis slender, terete, finely striate; branches 1- to 3-nate, slender, 1–7 cm. long, often bare of spikelets for 1–2 cm. near the base, somewhat hairy near the junction with the rhachis, finely spinulously ciliolate on the branchlets, but otherwise glabrous. *Racemes* 2- to 4-noded, 1–1·5 cm. long; internodes and pedicels slender, similar, 2·5–4 mm. long, often somewhat purplish in colour, ciliate with whitish hairs 0·5–1 mm. long. *Sessile spikelets* oblong-lanceolate, acuminate, 5·5–6·5 mm. long, 1·5–2 mm. wide, awned, straw yellow to fulvous or purplish, sparsely whitish or fulvously hairy, at length glabrescent except along the sides; callus shortly bearded. *Glumes* subcoriaceous; lower 12- to 13-nerved (5–6 evident near the tip), with a few cross-nerves about the middle, 2-keeled from near the middle, spinulously ciliolate on the scarious finely marginate keels, which end in minute but sometimes obscure teeth below the hyaline apex; upper 7-nerved, with a few cross-nerves in the upper half, slightly scabrid on the keel in the upper third. *Lemmas* moderately ciliate; lower elliptic-lanceolate, 5·5 mm. long, 1·8 mm. wide, finely 2-nerved; upper elliptic-ovate, 3·5–4 mm. long faintly 1- to 3-nerved, 2-lobed, with an awn 12–14 mm. long. *Anthers* 3·5 mm. long. *Grains* (immature) elliptic, 1·5 mm. long. *Pedicelled spikelets* usually ♂, linear-lanceolate to subulate, 6–7 mm. long; deciduous; lower glume 9- to 12-nerved, upper 6- to 8-nerved; anthers 3–3·5 mm. long.



Sorghum pugionifolium Snowden. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view. A, × 5; B and C, × 10. (From *Drummond* 21091.)

The type of this species is a specimen in Kew Herbarium, *Drummond* 21,091, collected on 24 October 1886, at Gurgáon, Punjab, India.

DIAGNOSTIC CHARACTERS AND AFFINITIES

The most significant characters of *S. pugionifolium* are the slender culms, not much over half a metre high; the short, narrow, 'dagger-shaped' leaves, 4–10 cm. long, 3–9 mm. wide; the small panicles 4–12 cm. long, 1–2 cm. wide; and the oblong-lanceolate, acuminate, sessile spikelets, 5·5–6·5 mm. long, 1·5–2 mm. wide, with awns about 12–14 mm. long. This species seems most closely allied to *S. somaliense*, but it differs from that species in the more slender culms, smaller different-shaped leaves, and the oblong-lanceolate, acuminate, sessile spikelets with their thinner subcoriaceous glumes.

DISTRIBUTION AND UTILITY

The type specimen, collected by Drummond at Gurgáon, in the Punjab, India, is the only one I have seen at Kew that belongs to this species and no information is available as to its utility. It is unlikely to prove of much economic value owing to its small size and scanty foliage. It is interesting, however, in its occurrence so far away from the usual distribution of the wild Sorghums belonging to the subsection *Arundinacea*. Its nearest relative and neighbour, *S. somaliense*, from Somaliland, is separated from it by Saudi Arabia, Iran and Baluchistan. As so few Sorghums have been recorded from these areas, however, it seems possible that further records of these two species may eventually come to hand to close the gap at present existing between them.

14. **Sorghum brevicarinatum** Snowden

Sorghum brevicarinatum Snowden, sp.nov.; a *S. verticillifloro* (Steud.) Stapf laminis foliorum latioribus, usque ad 5 cm. latis, spiculis sessilibus minoribus elliptico-ovatis acutis vel acuminatis 4·5–5·5 mm. longis 2–2·5 mm. latis, gluma inferiore breviore bicarinata carinis latiore marginatis differt.

Gramen annuum vel raro perenne, laxe caespitosum, 1·5–3·5 m. altum. *Culmi* robusti, prope basin 0·5–1 cm. lati, laeves vel tenuiter striati, simplices vel superne ramosi. *Folia* 5–10; laminae lineares, basi latae vel raro tenuiter angustae, in apicem longe acuminatum attenuatae, maturae plerumque 25–85 cm. longae, 2·5–5 cm. latae, prope vaginam et ligulam hirsutae, ceterum glabrae, marginibus superne spinuloso-scabridis, nervo medio pallido prominente infra prope basin. *Panicula* lanceolata, elliptico-lanceolata, vel ovata, laxa, 15–60 cm. longa, 10–25 cm. lata; axis primarius basin versus teres et plerumque laevis, superne canaliculatus angulis nonnunquam spinuloso-scabridis; rami graciles, 1–5-nati, primo suberecti sed mox diffusi, prope basin et axillis ramulorum hirsuti, superne scabridi; inferiores 15–30 cm. longi, basin versus ramosi vel per 5–10 cm. nudati. *Racemi* fragiles, 2–5-nodis, 1–2·5 cm. longi; rhacheos internodia gracilia, 2·5–3·5 mm. longa, pilis fere subalbidis 0·5–1 mm. longis dense ciliata; pedicelli internodiis similes vel nonnunquam graciliores. *Spiculae sessiles* elliptico-ovatae, acutae vel acuminatae, 4·5–5·5 mm. longae, 2–2·5 mm. latae, aristatae, eburneo-flavae, fulvae, vel demum badiae, purpureae, vel nigrae, omnino strigoso-hirsutae vel dorso glumarum demum glabrescentes et nitentes; callus copiose barbatus. *Glumae* aequales, apice subherbaceo excepto, coriaceae; inferior 9–11-nervis, triente superiore breviter bicarinata, carinis late marginatis, spinuloso-ciliolatis, dentibus minutis plerumque terminatis; superior 7-nervis, tertia parte superne acute carinata, carina scabrida. *Lemmata* tenuiter ciliata; inferius elliptico-oblongum vel elliptico-ovatum, 4–5 mm. longum, 2-nerve; superius ovatum vel ovato-ellipticum, 3–4 mm. longum, 3-nerve, breviter bilobum, arista 5–15 (raro 18) mm. longa. *Antherae* 2·5–3 mm. longae. *Caryopsides* obovato-ellipticae vel obovatae, 1·5–3 mm. longae, 1–2 mm. latae, brunneae, rubido-brunneae, vel brunneo-purpurascentes. *Spiculae pedicellatae* linearis vel lineari-lanceolatae, 4–6 mm. longae, ♂ vel plus minusve redactae, deciduae; gluma inferior 8–11-nervis, gluma superior 5–7-nervis; antherae 1·5–2·5 mm. longae.

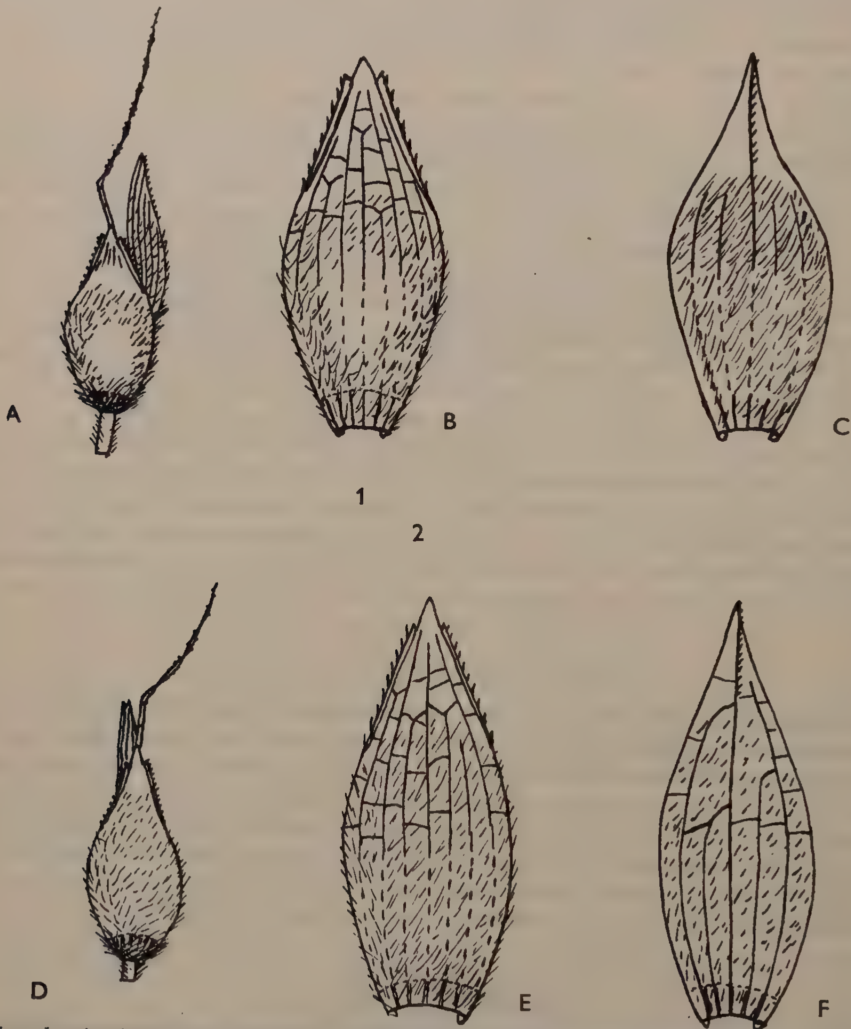
An annual or rarely a loosely tufted perennial, 1·5–3·5 m. high. *Culms* stout, 0·5–1 cm. wide near the base, smooth or sometimes finely and shallowly striate, simple or branched above, glabrous except near the nodes. *Leaves* 5–10; blades linear, mostly 25–85 cm. long and 2·5–5 cm. wide when mature, from a rather broad or sometimes slightly narrowed base tapering upwards to a fine point, greenish, sometimes rather glaucous, often flushed with brownish to reddish purple, with the paler mid rib prominent below near the base. *Panicle* lanceolate to elliptic-lanceolate or ovate, loose, 15–60 cm. long, 10–25 cm. wide; rhachis terete and more or less smooth below, strongly channelled and sometimes spinulously scabrid on the ridges upwards; branches slender, at first suberect but soon spreading, the lower 2–5 from each node, often 15–30 cm. long, branched near the base or often bare of spikelets for 5–10 cm., hairy near the base and in the axils of the rather widely scattered and scabrid branchlets. *Racemes* fragile, 2- to 5-noded, 1–2·5 cm. long; internodes slender, 2·5–3·5 mm. long, densely ciliate with mostly whitish hairs 0·5–1 mm. long; pedicels similar to the internodes or sometimes rather more slender. *Sessile spikelets* elliptic-ovate, acute or acuminate, 4·5–5·5 mm. long, 2–2·5 mm. wide, cream to tawny or at length mahogany red to maroon or black, permanently whitish strigose or at length glabrous and shining on the backs of the glumes; awned; callus copiously bearded. *Glumes* coriaceous almost throughout but with thinner tips; lower 9- to 11-nerved (with 3–5 nerves obscurely visible between the keels), shortly keeled in the upper third with the broadly margined keels spinulously ciliolate and gradually widening upwards until they terminate in minute teeth below the hyaline apex; upper 7-nerved, sharply keeled in the upper third, scabrid on the keel. *Lemmas* finely ciliate; lower elliptic-oblong to elliptic-ovate, 4–5 mm. long, 2-nerved; upper ovate to ovate-elliptic, 3–4 mm. long, 3-nerved; shortly 2-lobed, with an awn 5–15 (rarely 18) mm. long. *Anthers* 2·5–3 mm. long. *Grains* obovate-elliptic to obovate, 1·5–3 mm. long, 1–2 mm. wide, brownish to reddish brown or brownish purple; embryo-mark more or less obvious. *Pedicelled spikelets* linear to linear-lanceolate, 4–6 mm. long, ♂ or somewhat reduced, deciduous; lower glume 8- to 11-nerved, upper 5- to 7-nerved; anthers 1·5–2·5 mm. long.

Diagnostic characters and affinities

The distinguishing features of *S. brevicarinatum* are the small elliptic-ovate, acute to acuminate sessile spikelets, 4·5–5·5 mm. long, 2–2·5 mm. wide, with rather short keels which gradually widen upwards to end in more or less distinct minute teeth; and the broad leaves, mostly 2·5–5 cm. wide when mature. It is closely related to *S. verticilliflorum*, but most specimens can be readily separated from the latter species by the smaller elliptic-ovate sessile spikelets, with shorter, usually wider-margined keels, and the broader mature leaves. Intermediate states, such as may sometimes result from cross-fertilization with related species, are more difficult to determine.

Distribution and utility

As far as is at present known the distribution of this species extends from the Tana River in north-eastern Kenya Colony southwards along the coastal districts of Kenya and Tanganyika Territory as far as Useguha and Usagara districts, as well as to most of the nearby islands in the Indian Ocean, including those of Zanzibar, Seychelles, Comoros, Madagascar, and the Mascarenes. Most of the specimens from the mainland of Africa have been collected at low altitudes between 100 and 760 m. above sea-level. The majority of those enumerated below were found growing in or near cultivated lands, often close to the banks of rivers or sometimes in irrigation ditches, generally on alluvial soils or the sticky black soils often referred to as Black Cotton Soils. *S. brevicarinatum* readily intercrosses with the varieties of grain Sorghums cultivated in the districts where it is found, especially varieties of *S. roxburghii*. The grains of the wild plants are sometimes eaten by the natives in times of famine. No information is available regarding its use as fodder for domestic animals, but it should have about the same value as *S. verticilliflorum*, with which it has hitherto been identified. It may prove more suitable than the latter species for hot humid districts, as it would appear to have adapted itself more particularly to such conditions. There is no evidence on record as to its particular toxic properties, but these are not likely to differ much from the related *S. verticilliflorum*.



(1) *Sorghum brevicarinatum* var. *brevicarinatum* Snowden. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view. (From *Sampson* 99.) A, × 5; B and C, × 10. (2) *S. brevicarinatum* var. *swahilorum* Snowden. D, sessile and pedicelled spikelets; E, lower glume; F, upper glume, exterior view. D, × 5; E and F, × 10. (From *Sampson* 43.)

(i) Var. **brevicarinatum**

Var. **brevicarinatum**, based on *S. brevicarinatum* Snowden.

Sessile spikelets elliptic-ovate, acute, 4·5–5 mm. long; lower glume distinctly 2-keeled with the margins of the keels widening upwards to end in minute but distinct teeth; pedicelled spikelets often reduced, usually neuter, rarely ♂ with the anthers small.

The type of this variety is the same as that of the species, namely a specimen in Kew Herbarium, *Storey* 2, collected in Tanganyika Territory, on the Muhesa–Amani Road, at an altitude of 240 m.

KENYA COLONY. Tana River district, at Taneka, 760 m., *Sampson* 99!

TANGANYIKA TERRITORY. Usambara district, Muhesa–Amani Road, 240 m., *Storey* 2! Usagara district, Kilosa, *Burtt* 138!

A specimen from Wagamoya near Tongwe, *Storey* 12! which is damaged by 'Smut disease', probably belongs here.

ZANZIBAR. Wanda country, *Taylor* 93B! Yozani, near Pandanus forest, *Greenway* 1343! Without precise locality, *Vaughan* 1899!

SEYCHELLE ISLANDS. Mahé Island: *Neville*! *Thomasset*! Silhouette Island: *Gardiner*! Praslin Island: *Dupont*!

COMORO ISLANDS. Johanna Island, *Hildebrandt* 1716!

MADAGASCAR. Central Madagascar, *Baron* 2385! 4568! Nosi Bé, collected 1849, *Boivin* 1987!

RODRIGUEZ. Without precise locality; collected 1864–5, *Bouton* G73! Collected 1874, *Balfour*!

SOUTH AFRICA. Transvaal Province: Doornkloof, Irene, *Pole Evans* 337! This specimen was probably grown from introduced seed.

(ii) Var. **swahilorum** Snowden

Var. **swahilorum** Snowden, var.nov.; Spiculae sessiles elliptico-ovatae, acuminatae, 5–5·5 mm. longae; gluma inferiore moderate bicarinata, carinis sine dentibus vel in dentibus obscuris terminatis; spiculae pedicellatae plerumque ♂, antherae 1·5–2·5 mm. longae.

Sessile spikelets elliptic-ovate, acuminate, 5–5·5 mm. long; lower glume 2-keeled with the keels ending without teeth or obscurely toothed; pedicelled spikelets usually ♂, anthers 1·5–2·5 mm. long.

The type of this variety is *Greenway* 1956 in Kew Herbarium. It was collected in the Usambara district of Tanganyika Territory, at Tengeni, at an altitude of 210 m.

KENYA COLONY. Teita district, Voi, 610 m., *McDonald* 852! Malindi district, Chonyi, 270 m., *Taylor* 1219! Tana River district, Ngwena, *Sampson* 43!

TANGANYIKA TERRITORY. Arusha district, Mgaruki, *St Clair Thompson* 298! Usambara district: Tanga, *Holst* 2342! Lunguza, up to 600 m., *Greenway* 766 (sheet 1)! Tengeni, 210 m., *Greenway* 1956! Korogwe, in the Luengera valley, 450 m., *Davis* 1003! Useguha district, Morogoro, 450 m., *Rounce* 489! Mahenge district, 270–305 m., *Schlieben* 1710! Without precise locality, *Busse* 140!

The second sheet of *Greenway* 766 has been damaged by a 'Smut disease'.

COMORO ISLANDS. Mohilla Island, collected 1861, *Kirk*!

RÉUNION (BOURBON). Without precise locality, collected 1846, *Boivin* 991!

MAURITIUS. In forests, collected 1864–5, *Bouton*!

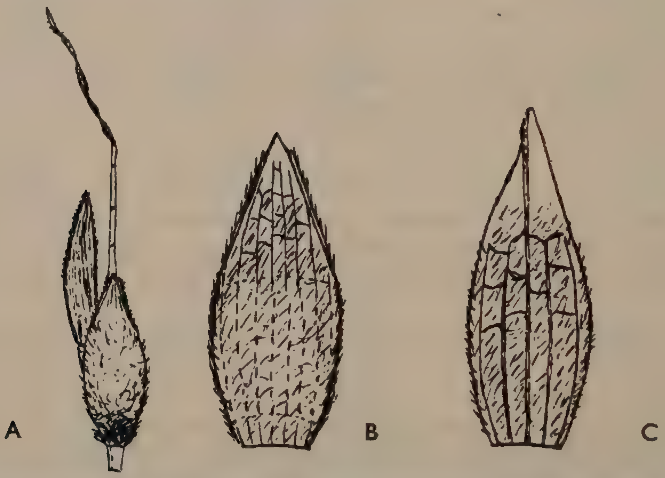
JAVA. Cultivated at Pasoervean, introduced from Amani, Tanganyika Territory, *Posthumus* 8 (3245)!

15. **Sorghum usambarense** Snowden

Sorghum usambarense Snowden, sp.nov.; affine *S. verticillifloro* (Steud.) Stapf et *S. brevicarinato* Snowden, ab illo laminis foliorum latioribus 3–5 cm. latis, panicula profusiore ramosa, spiculis sessilibus minoribus elliptico-lanceolatis vel elliptico-oblongis obtusis vel subacutis 4·5–5·2 mm. longis 1·5–2 mm. latis, ab hoc ramis paniculae gracilioribus magis numerosis, spiculis sessilibus angustioribus elliptico-lanceolatis vel elliptico-oblongis obtusis vel subacutis 1·5–2 mm. latis differt.

Gramen laxe caespitosum, 2–3·5 m. altum, perenne. *Culmi* validi, usque ad 1 cm. lati,

simplices vel superne ramosi, ad nodos pubescentes ceterum glabri. *Folia* numerosa; laminae lineares, e basi magis minusve contractae, longe in apicem tenuem attenuatae, 25–75 cm. longae, 3–5 cm. latae, ad margines serrulato-scaberrimae, costa media virido-albida superne gradatim tenuiter attenuata. *Panicula* laxa, lanceolata vel elliptico-lanceolata, 30–60 cm. longa, 10–15 cm. lata; axis primarius canaliculatus, angulatus, ad angulos spinuloso-scabridus; rami numerosi, parte basali excepta gracillimi, flexuosi et nutantes, superne ut ramuli scaberrimi, prope basin et axillis ramulorum hirsuti, inferiores plerumque 5–6-nati, 15–28 cm. longi, basin versus per 5–10 cm. nudati. *Racemi* fragiles, 2–5-nodis, 1–2 cm. longi; rhacheos internodia gracilia, 2–3·5 mm. longa, pilis plerumque rufis 0·5–1 mm. longis dense ciliata; pedicelli internodiis similes. *Spiculae sessiles* elliptico-lanceolatae vel elliptico-oblongae, obtusae vel subacutae, 4·5–5·2 mm. longae, 1·5–2 mm. latae, aristatae, stramineo-flavae vel fulvae, demum rubido- vel brunneo-purpureae, pilis fulvis, rufis vel purpureis dense strigosae, vel interdum dorso glumarum glabrescentes; callus dense barbatus. *Glumae* aequales, parte apicali et prope callum excepta, coriaceae; inferior plerumque 11-nervis, supra medium tenuiter bicarinata, carinis breve spinuloso-ciliolatis plerumque dentibus minutis terminatis; superior dorso anguste convexo, 7-nervis (2–4-nervis brevis), apicem versus acute carinata, carina scabrida. *Lemmata* tenuiter ciliata; inferius elliptico-lanceolatum, 4·3–4·8 mm. longum, plerumque 2-nerve; superius ovatum vel ovato-ellipticum, 3–3·5 mm. longum, 3-nerve, breviter bilobum, arista 12–15 mm. longa. *Lodiculae* sparse ciliolatae vel paene glabrae. *Antherae* 3 mm. longae. *Caryopsides* (immaturae) ellipticae vel obovato-ellipticae, circiter 1·5 mm. longae et 0·8 mm. latae, rubido-brunneae. *Spiculae pedicellatae* lineari-lanceolatae vel subulatae, 4·5–5·5 mm. longae, ♂, deciduae; gluma inferior 9–11-nervis, gluma superior 5–7-nervis; antherae 2–3 mm. longae.



Sorghum usambarense Snowden. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view. (From *Eichinger* G 5885.) A, × 5; B and C, × 10.

A loosely tufted short-lived perennial, 2–3·5 m. high. *Culms* stout, up to 1 cm. wide, simple or branched above, glabrous except for the pubescent nodes. *Leaves* many; blades linear, 25–75 cm. long, 3–5 cm. wide, from a rounded and somewhat constricted base, gradually narrowing upwards to the finely pointed apex, with the greenish white mid rib gradually becoming very fine near the tip, and the margins serrulately scabrid almost to the base. *Panicle* loose, lanceolate to elliptic-lanceolate, 30–60 cm. long, 10–15 cm. wide; rhachis channelled and angular, usually coarsely spinulously scabrid on the ridges, especially in the upper half; branches numerous, very slender and flexuous with the tips soon drooping, the lower usually 5–6 from each node, 15–28 cm. long, often

naked for 5–10 cm. from the base, very rough upwards like the branchlets, hairy at the base and in the axils of the divisions. *Racemes* fragile, 2- to 5-noded, 1–2 cm. long; internodes and pedicels slender, 2–3·5 mm. long, densely ciliate with usually rufous hairs 0·5–1 mm. long. *Sessile spikelets* elliptic-lanceolate to elliptic-oblong, obtuse or subacute, 4·5–5·2 mm. long, 1·5–2 mm. wide, awned, straw yellow to fulvous or at length reddish to brownish purple, usually densely strigose with tawny to rufous or purplish hairs, but sometimes glabrous on the backs of the glumes; callus densely bearded. *Glumes* coriaceous, but slightly thinner near the tips and just above the callus; lower usually with 11 primary nerves (3–4 nerves evident near the tip), keeled from a little above the middle with the narrow linear margins of the keels usually ending in minute teeth below the rather short hyaline tip, shortly spinulously ciliolate on the keels; upper narrowly convex, 7-nerved, with 2–4 of the inner lateral ones usually rather short, sharply keeled and scabrid towards the tip. *Lemmas* finely ciliate; lower elliptic-lanceolate, 4·3–4·8 mm. long, usually 2-nerved; upper ovate to ovate-elliptic, 3–3·5 mm. long, 3-nerved, shortly 2-lobed, awn 12–15 mm. long. *Lodicules* sparsely ciliolate or almost glabrous. *Anthers* 3 mm. long. *Grains* (immature) elliptic to obovate-elliptic, about 1·5 mm. long and 0·8 mm. wide, reddish brown. *Pedicelled spikelets* linear-lanceolate to subulate, 4·5–5·5 mm. long, ♂, deciduous; lower glume 9- to 11-nerved, upper 5- to 7-nerved; anthers 2–3 mm. long.

This species is based on specimens collected in the Usambara district of Tanganyika Territory. Of these I have selected *Eichinger* G5885 in Kew Herbarium as the type.

DIAGNOSTIC CHARACTERS AND AFFINITIES

The chief characters which serve to distinguish this species are the broad leaves, 3–5 cm. wide when mature, the large loose panicle with long slender branches in clusters often 5–6 or more from a node, and the small narrow elliptic-lanceolate to elliptic-oblong sessile spikelets, 4·5–5·2 mm. long, 1·5–2 mm. wide, with obtuse to subacute tips. *S. verticilliflorum* var. *infrequens* is the species most closely related to it, especially in the size and colouring of the sessile spikelets, but these are somewhat larger and the tips more acuminate than in those of *S. usambarense*. The latter also differs in the broader leaves as well as usually having a larger panicle with longer slender branches often 5–6 or more from each of the lower nodes. *S. usambarense* is easily separated from the related broad-leaved *S. brevicarinatum* by the narrow elliptic-lanceolate to elliptic-oblong sessile spikelets.

DISTRIBUTION AND UTILITY

S. usambarense has so far been recorded only from the warmer parts of the Usambara district of Tanganyika Territory, within a short distance of Amani. It appears to be confined mainly to cultivated lands such as are abandoned and become overgrown, especially those near rivers. There is no evidence of its cultivation for fodder, but it would appear to be of about the same value for that purpose in hot humid districts as *S. brevicarinatum*.

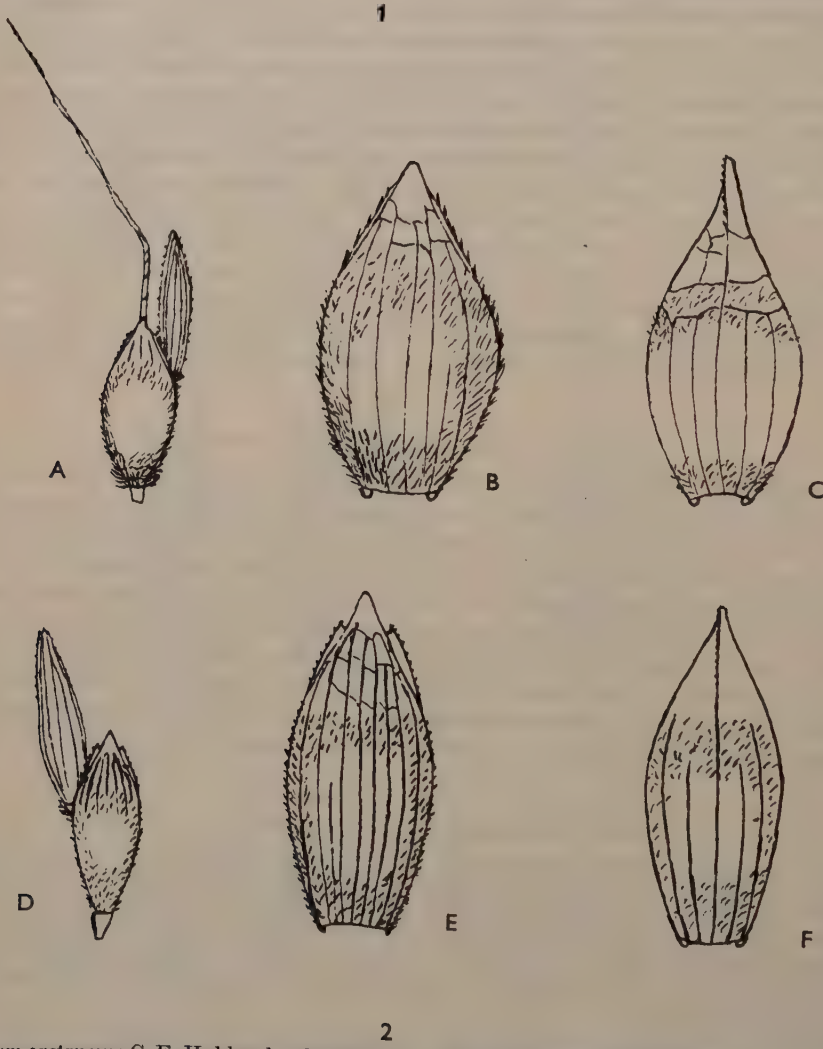
TANGANYIKA TERRITORY. Usambara district: Amani, in the warmer parts of old cultivations, *Eichinger* G 5885! 7642! s.n.! Near the Kihuku River, a 12 ft. high tussock grass, *Greenway* 3245!

16. **Sorghum castaneum** C. E. Hubbard et Snowden

Sorghum castaneum C. E. Hubbard et Snowden in *Kew Bull.* p. 316, 1936. The basis of this species is a specimen in Kew Herbarium, collected in the Toro district of Uganda, at Bubandi, 1050 m., in Elephant Grass country, *Thomas* 714.

Description

A loosely tufted perennial up to about 2·5 m. high. *Culms* stout, up to 8 mm. wide near the base, simple or branched. *Leaves* 6–7 or more; blades linear, from a broad base tapering to a pointed apex, up to 40 cm. long, 1·5–2·7 cm. wide, green, sometimes slightly glaucous, blotched with purplish colouring. *Panicle* lanceolate- to ovate-oblong, about 40 cm. long and 10–15 cm. wide, loose; rhachis somewhat angular and widely grooved, densely hairy at the nodes; branches 2–4 or sometimes solitary, slender, flexuous, hairy in the axils of the divisions, scabrid upwards, the lower ones up to 20 cm. long, usually bare of spikelets for 5 cm. or more from the hairy base. *Racemes* fragile, 2- to 5-noded, up to 15 mm. long, internodes and pedicels slender, 2–3·5 mm. long, densely ciliate with fulvous hairs. *Sessile spikelets* broadly elliptic to elliptic-oblong, obtuse, 4–4·5 mm. long, 2–2·5 mm. wide, chestnut to dark brown or brownish black, permanently hirsute or



(1) *Sorghum castaneum* C. E. Hubbard et Snowden. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view. (From *Thomas* 714.) (2) *S. panicoides* Stapf. D, sessile and pedicelled spikelets; E, lower glume; F, upper glume, exterior view. (From *Figari*, Abyssinia.) A and D, × 5; B, C, E and F, × 10.

glabrescent on the backs of the glumes, awned; callus shortly bearded. *Glumes* coriaceous with slightly thinner tips; lower at length slightly bulging in the lower half, 8- to 11-nerved (with about 3 nerves visible near the tip), cross-nerves few and obscure, 2-keeled in the upper third, spinulously ciliolate on the finely margined keels which merge into the hyaline apex or rarely end in obscure teeth near the tip; upper glume strongly convex, 7-nerved, with the inner lateral ones short, a few faint cross-nerves above the middle, sharply keeled near the tip, usually scabrid on the keel. *Lemmas* finely ciliate; lower elliptic-ovate or elliptic, 4–4·3 mm. long; upper ovate to ovate-oblong, 3 mm. long, shortly bilobed, awn 9–12 mm. long. *Anthers* 2·5 mm. long. *Grains* obovate to obovate-rotund, 2–2·5 mm. long, 1·5–1·7 mm. wide, brownish purple; embryo-mark obscure to distinct. *Pedicelled spikelets* 4–4·5 mm. long, ♂ or sometimes reduced, tardily deciduous; lower glume 8- to 9-nerved, upper 5- to 8-nerved; anthers small.

Diagnostic characters and affinities

S. castaneum may be recognized by the small broadly elliptic to elliptic-oblong sessile spikelets 4–4·5 mm. long, 2–2·5 mm. wide, with obtuse tips, usually hairy and chestnut to dark brown or brownish black in colour. It has narrow leaves resembling those of *S. verticilliflorum*, but from this species it is easily separated by its smaller, broad, obtuse sessile spikelets, the lower glume fewer-nerved, and the upper glume with shorter inner lateral nerves. The narrow leaves serve to distinguish *S. castaneum* from the broad-leaved *S. brevicarinatum* and *S. usambarense*, but in addition the sessile spikelets are smaller, broader elliptic, and more obtuse than the former, and are wider than the latter, whilst the fine keel-margins usually merge into the hyaline apex without distinct teeth.

Distribution and utility

No further specimens to match this interesting species have been received since the original gathering and it would appear that its distribution may be confined to the Bwamba area of the Toro district. This lies to the west of the Ruwenzori mountains, in the valley of the River Semliki, adjoining the Belgian Congo, which is reputed to be unhealthy, sparsely populated by the natives, and seldom visited by Europeans. It seems possible that *S. castaneum* may have originated from cross-fertilization between *S. verticilliflorum* and the local cultivated grain Sorghums, which belong mainly to *S. nigricans*, which it somewhat resembles in the smallness and shape of the sessile spikelets. On the other hand, it may be one of the primitive types from which *S. nigricans* has been evolved. *S. castaneum* is said to be frequent in areas where Elephant Grass (*Pennisetum purpureum* Schumach.) is prevalent, which suggests a preference for a habitat where there is an evenly distributed rainfall and a well-drained fertile soil. Its utility is probably somewhat similar to that of *Sorghum verticilliflorum*, although up to now it does not appear to have been specially cultivated for use as fodder, but is grazed by wild and domestic animals in the localities where it grows naturally.

Uganda. In Bwamba county of Toro district, at Bubandi, 1050 m., *Thomas* 714!

17. **Sorghum panicoides** Stapf

Sorghum panicoides Stapf in Prain, *Fl. Trop. Afr.* 9, 120, 1917, is based on a specimen collected in eastern Abyssinia by *Figari*, the type specimen being in Kew Herbarium.

Description

Probably an annual, but base unknown. *Culms* 3·5 mm. thick just below the panicle. *Leaves* few (only the uppermost seen); ligule about 2 mm. long, fringed with stiff hairs; blades linear, from a fairly wide base tapering upwards to the acuminate tip, about 35 cm. long, 1·5–2 cm. wide, green, but with reddish colouring towards the margins, hairy behind the ligule, mid rib stout below. *Panicle* narrowly oblong to oblong-lanceolate, 20–25 cm. long, 6 cm. or more wide, somewhat contracted or loose; branches suberect or spreading, very slender and flexuous, the lower several in a whorl, up to 15 cm. long, often bare for 1–6 cm. from the hairy base or sometimes undivided for half their length, very finely scabrid above, almost smooth below. *Racemes* up to 5-noded and 2 cm. long; internodes and pedicels very slender, 3–3·5 mm. long, ciliate with whitish hairs 0·5–0·75 mm. long. *Sessile spikelets* elliptic to elliptic-oblong, subacute, 4–5 mm. long, 1·5–2 mm. wide, dull cream to buff yellow with 4–5 nerves visible in the upper half of the lower glume when young, sparsely hairy with whitish hairs, especially near the base, above the middle, and along the sides, awnless; callus moderately bearded with whitish hairs 1 mm. long. *Glumes* thinly coriaceous up to the middle, very thin and papery above; lower usually 11-nerved, with a few faint cross-nerves towards the tip, shortly 2-keeled in the upper third, with the narrow margins widening upwards to end in minute teeth, forming with the hyaline apex a distinctly 3-toothed tip; upper delicately 7- to 8-nerved, with the inner lateral ones rather short, cross-nerves absent or obscure, finely keeled and scabrid on the keel in the upper fourth. *Lemmas* thinly ciliate; lower elliptic- to oblong-lanceolate, 4–4·5 mm. long; upper ovate, 3 mm. long, subentire, 1- to 3-nerved, with a small mucro up to 0·5 mm. long. *Anthers* 2·5–3 mm. long. *Ovary* elliptic, mature grains unknown. *Pedicelled spikelets* 4·5–6 mm. long, ♂, deciduous; lower glume 7- to 8-nerved, upper 6- to 7-nerved; anthers 2·5–2·8 mm. long.

DIAGNOSTIC CHARACTERS AND AFFINITIES

The distinguishing characters of *S. panicoides* are the narrow elliptic to elliptic-oblong, subacute sessile spikelets, 4–5 mm. long, 1·5–2 mm. wide, the unusually thin glumes with the nerves of the lower glume outwardly visible to the middle, the short keels of the lower glume with the narrow margins widening upwards to end in minute teeth and form with the hyaline apex a distinctly 3-toothed tip, and the awnless upper lemma. It does not appear to be closely related to any of the other species in this subsection *Arundinacea*, differing from them all in the thinner glumes and the upper lemma with a very small mucro. The thinner glumes, the lower usually with 11 or more primary nerves, also separate it from most of the awnless forms of the subsection *Halepensia*, particularly those of *S. halepense*, which it somewhat resembles in the size and shape of the sessile spikelets. The absence of the base of the culm, and mature leaves from the centre of the culm, as well as of mature grains, add to the difficulties of determining the relationship of this species.

DISTRIBUTION AND UTILITY

No other specimens have been identified with *S. panicoides* except the original plant collected in Abyssinia. It does not appear to have been grown for fodder or to have any special merit for this purpose.

ABYSSINIA. In east Abyssinia, without precise locality or number, *Figari*!

Piper (in *Proc. Biol. Soc. Wash.* 28, 29, 1915) mentions the above specimen in a note under *Andropogon halepensis muticus*, but Stapf (in Prain, *Fl. Trop. Afr.* 9, 120, 1917) evidently considered it to be an annual and a distinct species (belonging to the subsection *Arundinacea*). After careful examination of the scanty material available at Kew I find no reason to disagree with Stapf's conclusions.

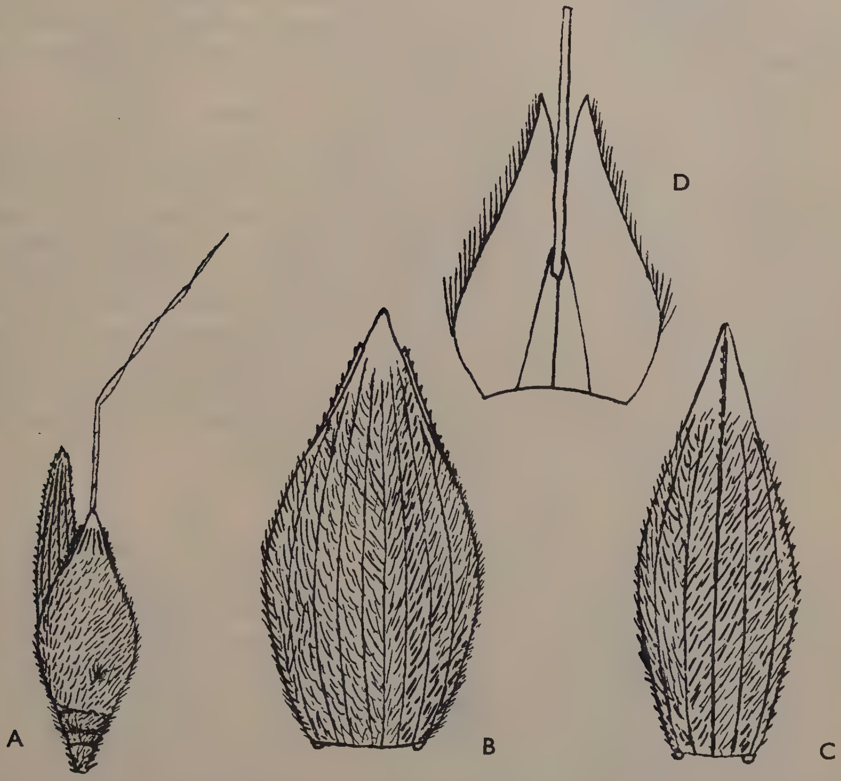
18. **Sorghum hewisonii** (Piper) Longley

Andropogon sorghum hewisoni Piper in *Proc. Biol. Soc. Wash.* 28, 41, 1915, is founded on a specimen, grown in the United States, which was raised from seed collected by Hewison from wild plants in the Sennar district of the Blue Nile province, in the Anglo-Egyptian Sudan. I have not been able to see the type, which Piper states was grown in a greenhouse, but I have examined an authentic specimen, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 33,739, collected by Reed on 31 Oct. 1916, which was raised at Chula Vista, California, from the same batch of seed as the type specimen.

Sorghum hewisonii (Piper) Longley in *J. Agric. Res.* 44, 318, 319, 1932. This name was used by Longley in an account of the chromosomes of grass Sorghums. It is based on *A. sorghum hewisoni* Piper.

DESCRIPTION

A vigorous loosely tufted perennial, 2–3·5 m. high. *Culms* stout, 1–3 cm. wide near the base, solitary or few to many from the basal rootstock, simple or branched above, often coated with a thin waxy bloom. *Leaves* numerous, 12–20; sheaths mostly longer than the internodes; blades 0·7–1 m. long, 4–8 cm. wide, from a broad rounded base, narrowing upwards into a pointed apex, with the broad mid rib prominent below in the lower half. *Panicle* oblong to somewhat fusiform, dense and sometimes more or less compact, 10–20 cm. long, 3–8 cm. wide; rhachis often completely hidden by the branches and spikelets, channelled below, somewhat angular upwards, tomentose to hirsute; branches crowded, usually many from each node, rather stiff and suberect, the lower 5–10 cm. long, furnished with spikelets up to, or almost up to, the silkily hairy base. *Racemes* tough or tardily disintegrating, mostly 1- to 3-noded and 8–20 mm. long, internodes and pedicels rather slender to somewhat stout, 2–4 mm. long, densely ciliate with usually whitish hairs about 1 mm. long. *Sessile spikelets* ovate to broadly elliptic-ovate, acute to acuminate, 6–7·5 mm. long, 2·5–3·5 mm. wide, with about 4 greenish nerves



S. hewisonii (Piper) Longley. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view; D, upper lemma with lower part of awn. (From *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 33,739.) A, ×5; B–D, ×10.

visible between the keels of the lower glume when young, mostly straw yellow to deep cream or tawny, but sometimes chestnut red to maroon, usually densely strigose with fulvous to tawny or rarely pale purplish hairs, awned; callus bearded with hairs about 1 mm. long. *Glumes* firmly coriaceous but somewhat thinner near the tip where the nerves are obscurely visible; lower 11- to 15-nerved, often with obscure transverse nerves in the upper third or half, obscurely 2-keeled in the upper third and spinulously ciliolate on the narrow linear margins which end in minute teeth or merge gradually into the hyaline tip; upper 7-nerved, often with obscure cross-nerves in the upper half, scabrid on the keel in the upper third. *Lemmas* densely ciliate; lower elliptic-lanceolate to elliptic-oblong, 5–6·5 mm. long; upper ovate, 4–5 mm. long, 2-lobed to 0·5 or 1 mm. deep, awn 10–18 mm. long. *Anthers* 3–4 mm. long. *Grains* obovate-elliptic, 3·5–4·5 mm. long, 2·5–3 mm. wide, brownish yellow or light to dark reddish brown; embryo-mark distinct. *Pedicelled spikelets* 5–7 mm. long, ♂ or somewhat reduced, of similar colour to the sessile, usually persistent; lower glume 8- to 13-nerved, upper 5- to 10-nerved; anthers 2·5–3·5 mm. long.

Diagnostic characters and affinities

The broad leaves, 4–8 cm. wide; dense, sometimes more or less compact, panicle; somewhat tough racemes; and the large broadly elliptic-ovate to ovate, acute to acuminate, very hairy sessile spikelets, 6–7·5 mm. long, 2·5–3·5 mm. wide, are the most distinctive features of *S. hewisonii*. In the shape and hairiness of the sessile spikelets it is closely related to *S. aethiopicum*, but it is readily separated from the latter species by the taller, stouter culms; larger, wider leaves; more compact densely branched panicles; tougher racemes; and shorter awns. I do not think that it is closely related to any of the other wild Sorghums, but Piper (loc. cit) suggests that it is allied to specimens collected in the Anglo-Egyptian Sudan by *Brown* that were later referred by Stapf to *S. lanceolatum*. The lanceolate sessile spikelets, loose panicles and narrow leaves of this latter species, however, enable it to be easily distinguished from *S. hewisonii*.

Distribution and utility

Specimens of *S. hewisonii* have been found growing wild in the Anglo-Egyptian Sudan and its distribution may also extend into Abyssinia and Somaliland. In the United States, where seeds were introduced from the Anglo-Egyptian Sudan, Piper states that at Arlington Farm, Virginia, the plants grew 2–2½ m. high but did not bloom before frosts occurred and prevented further growth. This suggests that it either requires a long growing season or a hotter climate than that of Virginia, which may account for the fact that it does not appear to have been extensively grown in the United States. Nor is there any evidence of its having been cultivated for fodder in the Anglo-Egyptian Sudan, although its stout culms, furnished with abundant broad leaves, and its tough racemes, enabling the seed to be harvested without much loss, make it well suited for trial as a fodder crop in countries with a hot climate. The wild specimens have generally been found in or near to cultivated lands and the plants resemble a cultivated race more than a wild one.

Anglo-Egyptian Sudan. Darfur province, Shankletebiya, on Fasher–Nyala Road, *Harrison* 205! White Nile province, Degain and Tendelai, *Andrews* 1! 4! Makwar, Sept.–Dec. 1929 (Sheet 1) *Punter*! Seed from Khartoum (grown at Chula Vista, California), ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 33,739!

Vern. names: Addar, Adar (Arabic).

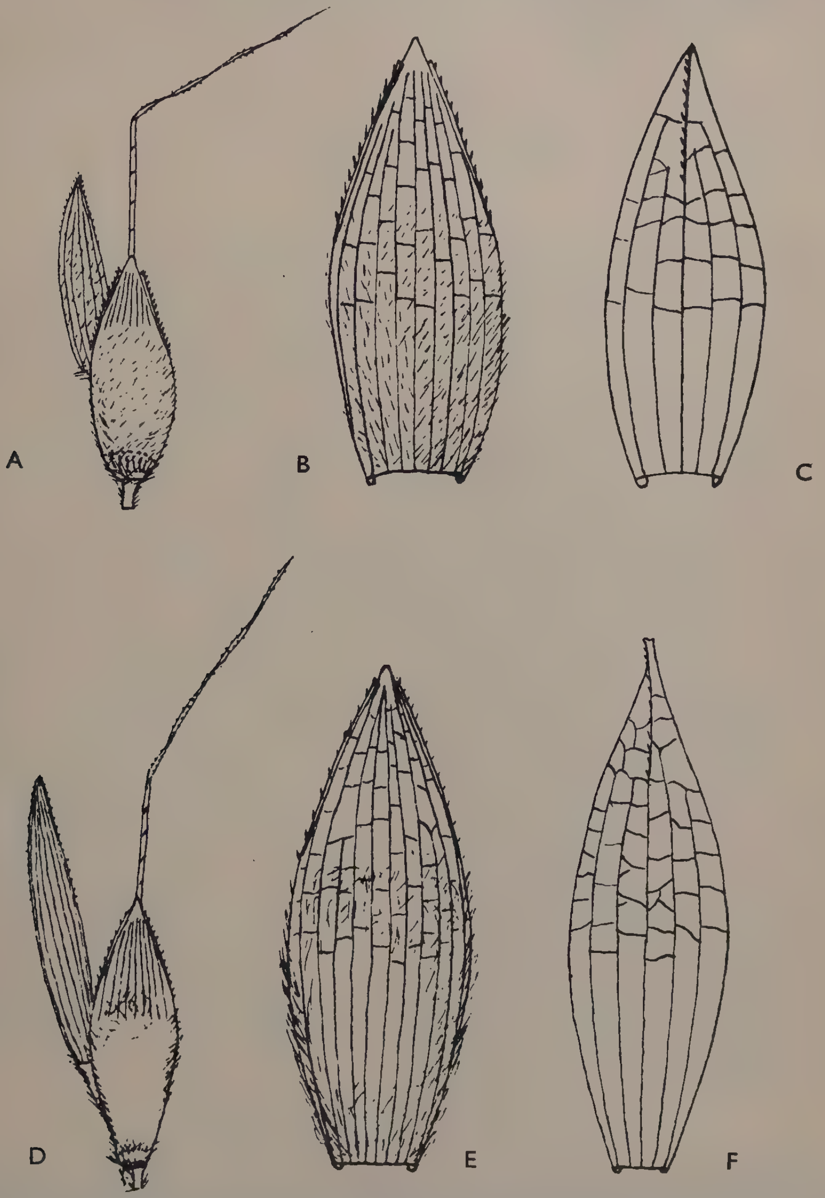
Eritrea. A specimen from Bogos, Cheren Dari, 1360 m. (ex Herb. R. Horti Romani) *Fiori* 1230! may belong here, but the material is inadequate for exact determination.

Somaliland. Without precise locality, *Collenette* 159!

This specimen has small somewhat immature spikelets but otherwise agrees well with *S. hewisonii*.

19. **Sorghum sudanense** (Piper) Stapf

Andropogon sorghum subsp. *sudanensis* Piper in *Proc. Biol. Soc. Wash.* **28**, 33, 1915, the basis of this species, was founded on a specimen grown in Virginia, United States of America, which was raised from seed obtained from the Anglo-Egyptian Sudan. Although I have not been able to see the type specimen, I have examined specimens grown at Arlington Farm, Virginia, raised from the same sample of Sudan seed as the type, that were sent to Kew by Piper, besides several others specimens at Kew determined by Piper as *Andropogon sorghum sudanesis.*



Sorghum sudanense (Piper) Stapf. A and D, sessile and pedicelled spikelets; B and E, lower glume; C and F, upper glume, exterior view. (A–C, from *U.S. Dep. Agric. Sorghum Herb.* ex. *Piper*; D–F, from *Potts* 2897.) A and D, × 5; B, C, E and F, × 10.

Holcus sorghum subsp. *sudanensis* (Piper) Hitchc. in *Proc. Biol. Soc. Wash.* **29**, 128, 1916, is a change of name, based on Piper's subspecies.

Sorghum sudanense (Piper) Stapf. in Prain, *Fl. Trop. Afr.* **9**, 113, 1917, is based on *Andropogon sorghum sudanensis* Piper.

Holcus sudanensis (Piper) Bailey, *Gentes Herb.* **1**, 132, 1923, has the same basis.

Andropogon sudanensis (Piper) Leppan & Bosman, *Field Crops of South Africa*, p. 286, 1923, is based on Piper's subspecies and gives it specific rank under the genus *Andropogon*.

Sorghum vulgare var. *sudanense* (Piper) Hitchc. in *J. Wash. Acad. Sci.* **17**, 147, 1927, is a change of name made on reducing Piper's subspecies to a variety of *Sorghum vulgare* Pers.

DESCRIPTION

An annual 1·5–3 m. high, or sometimes persisting as a loosely tufted perennial. *Culms* rather slender, about 3–6 mm. wide near the base, solitary or often several to many arising together from the basal rootstock. *Leaves* up to 9 or more; sheaths densely pubescent near the base; blades narrow linear, attenuated towards the base, 15–50 cm. long, 8–12 (rarely 15) mm. wide, narrowing upwards to a sharp point, dull to bright green, often blotched with purple, mid-rib rather stout and striate. *Panicle* ovate to pyramidal, very loose, 15–30 cm. long, 8–15 cm. broad; rhachis channelled and rough on the ridges upwards; branches ascending, soon spreading, slender and flexuous, the lower 2–5 from each node, 5–15 cm. long, often bare for 1–5 cm. from the almost glabrous base, spinulously scabrid upwards like the branchlets. Racemes usually tough, 2- to 5-noded, 1·5–2·5 cm. long; internodes slender, 2·5–4 mm. long, ciliate with whitish to fulvous or pale purplish hairs 0·5–0·75 mm. long; pedicels similar or sometimes a little shorter. *Sessile spikelets* elliptic to elliptic- or oblong-lanceolate, subacute, 6–7·5 mm. long, 2–3 mm. wide, pale straw or buff yellow to tawny, with about 5 greenish nerves visible between the keels of the lower glume when young, at length sometimes purplish to almost black, sparingly whitish to purplish strigillose but usually glabrous and shining on the backs of the glumes when mature, awned; callus beard scanty to moderate. *Glumes* coriaceous up to the middle or somewhat above the middle, thinner upwards; lower 11- to 15- (mostly 13-)nerved, with cross-nerves in the upper half, 2-keeled from just above the middle, obscurely margined or with the fine linear margins ending without or with only obscure teeth just below the short hyaline tip, spinulously ciliolate on the keels; upper 7-nerved, with cross-nerves from near the tip to below the middle, scabrid on the sharp keel in the upper fourth. *Lemmas* finely long-ciliate; lower elliptic-lanceolate to elliptic-oblong, 5–6·5 mm. long; upper ovate to ovate-elliptic, 3·5–4·5 mm. long, 2-lobed to 0·5 or 1 mm. deep, awn 10–16 mm. long. *Anthers* about 4 mm. long. *Grains* elliptic to obovate-elliptic, yellowish to tan 3·5–4·5 mm. long, 1·5–2 mm. wide; embryo-mark usually distinct. *Pedicelled spikelets* persistent, ♂ or sometimes neuter, 5·5–8 mm. long, greenish straw colour to tawny or purplish; lower glume 9- to 11-nerved, upper 7- to 9-nerved; anthers 3–4 mm. long.

DIAGNOSTIC CHARACTERS AND AFFINITIES

S. sudanense may be recognized by the narrow leaves; loose spreading panicle with tough racemes; persistent sessile and pedicelled spikelets, the sessile almost elliptic or elliptic- to oblong-lanceolate, subacute, 6–7·5 mm. long, 2–3 mm. wide, with awns 10–16 mm. long. It is probably most closely related to *S. lanceolatum* and *S. virgatum*, but it also resembles *S. verticilliflorum*. It can be distinguished from all of them by the tough racemes with persistent sessile and pedicelled spikelets, as well as by the shape of the sessile spikelets, which are broader in the upper half, more elliptic in outline, and subacute. The grains of *S. sudanense* are also comparatively large and usually rather long and narrow.

Distribution and utility

The natural distribution of *S. sudanense* seems to be confined to Egypt and the Anglo-Egyptian Sudan, although it does not appear to be common as a wild plant in either country, as comparatively few wild specimens have been recorded. Early in the twentieth century it was introduced into America. According to Piper (in *Proc. Biol. Soc. Wash.* **28**, 33, 1915) seeds from Khartoum, in the Anglo-Egyptian Sudan, were sent to the United States by Hewison. The resulting plants were successfully grown and after trial proved to be suitable as fodder for stock. Under the name of Sudan Grass the species was afterwards distributed and cultivated in many parts of the country. Since that time it has been introduced into many other countries, including those of South America, South Africa, and Australia, and is now extensively grown for feeding domestic animals. In the United States, where it is generally treated as an annual plant, if given enough room, it tillers freely and may produce as many as 100 stems from one crown. These tiller-shoots are most numerous after the first crop has been reaped and in consequence the hay obtained from the second cutting is often finer than that of the first. The absence of perennial rhizomes makes *S. sudanense* more suitable as a fodder crop than *S. halepense*, as the latter has proved to be a troublesome weed in many cultivated lands because of the difficulty in eradicating the rhizomes when the land is needed for other purposes. The tough racemes of *S. sudanense* make it possible to harvest the crop with little loss of seed, and this is another factor that has led to its replacing Johnson Grass (*S. halepense*) as a fodder crop in many countries where Sorghums are grown for feeding stock. *S. sudanense* readily intercrosses with cultivated Sorghums when grown in close proximity to them, especially with the sweet-stemmed varieties belonging to *S. bicolor* and *S. dochna*. Such hybrids have often been recorded in the United States as well as in Australia, but they are usually easily distinguished from the typical *S. sudanense* by their wider leaves and stouter culms.

S. sudanense is regarded as poisonous to stock under certain conditions. The HCN content is not constant, however, and is affected by drought, stunted growth, and frost damage, as well as by insect and fungous attack. According to Hurst (in *The Poison Plants of New South Wales*, 1942) it contains about two-fifths as much HCN as is found in the cultivated grain Sorghums. Swanson (in *J. Agric. Res.* **22**, 125–38, 1921; *J. Amer. Soc. Agron.* **5**, 13, no. 1, 33–36, 1921) dealing with hydrocyanic acid in Sudan Grass, found that although large amounts of the acid were generally present in Sudan Grass used for pasture no harm resulted to the cattle. The liberation of the acid was associated with enzyme action. Slow drying caused the hydrocyanic acid to disappear but making Sudan Grass into silage did not diminish the amount of acid present. Freshly frosted plants that were tested yielded very large amounts of hydrocyanic acid but the acid diminished rapidly as soon as the plants began to wilt and when they were dry it had disappeared. Although Sudan Grass giving a high content of hydrocyanic acid when tested was harmless under some conditions, under different conditions it proved harmful, but the immunity from harmful effects was not due to the animals becoming accustomed to feeding on Sudan Grass.

The toxicity of Sudan Grass has been investigated in various countries, especially in the United States, South Africa, and Australia. Full reports of these investigations have been published in the Agricultural, Veterinary, and Scientific Journals of the countries concerned. These should be referred to for fuller information on this important subject, as the investigators have not always obtained the same results, and there are still many factors which require further consideration and experimental investigation.

England. Cultivated in the Royal Botanic Gardens, Kew, in 1935, *Snowden*!

Turkey. Ankara (Jan. 32) *Kotte*!

Egypt. Nile banks, between Cairo and Keneh, *Schweinfurth* 1548! Cairo, *Herb. Hooker* (1867)! Upper Egypt, *Sieber*! Ismailia, *Muschler* (March, 1905)!

Vern. names: Garawa, Hashish el Sudan.

ANGLO-EGYPTIAN SUDAN. Grown at Arlington Farm, Virginia, from seed received from Khartoum, ex United States Sorghum Herb., *Piper*! Without precise locality, *Messrs Vilmorin* 452/1929! received Kew Sept. 1922, *Massey*! Halfa (Wadi Halfa?), in cultivations, *Meinertzhagen*!

A specimen from Kiling-Jebel Marra, 2100 m., *Steele*! is probably this species, but the spikelets are unusually hairy.

FRENCH SUDAN. El Oualadji, in irrigation channels, apparently spontaneous, but perhaps introduced for forage, *Chevalier* 43,917!

SOUTHERN RHODESIA. Victoria Falls, ex *U.S. Dep. Agric. Sorghum Herb. S.P.I.* 49,209! Without precise locality, ex *Dep. Agric. Herb.* 3034!

SOUTH AFRICA. Bloomfontein, introduced from North Central Africa, *Potts* 2897!

JAVA. Without precise locality, *Posthumus* 92!

AUSTRALIA. Queensland: Brisbane Botanic Gardens, *White* 11! Darling Downs, Inglewood—Milmarran, *White* 9736! Darling Downs, between Dulacca and Palardo, 305 m., *Blake* 7579! Redcliffe, near Brisbane, *Hubbard* 5535! Mileo, *Hubbard & Winders* 6404! Waterford, Moreton district, *Mead* 3! State Farm, Bungewogorai, *Soutter*! Barcaldine, *Stibbards*! Mitchell district, Terrick Terrick station, *Cameron*!

Two of the three sheets of *Hubbard* 5535, from Redcliffe near Brisbane, appear to have been cross-fertilized, one approaching forms of *Sorghum dochna*, and the other having the sessile spikelets only 5·5 mm. long. A specimen from the State Farm, Bungewogorai, *Soutter*, with broad leaves and short wide spikelets, may also be a hybrid between *S. dochna* and *S. sudanense*.

UNITED STATES. California: Shasta country, at Anderson, 130 m., in ditches along S.P. Railway, ex Herb. Univ. California, *Long* 79*a*!

20. **Sorghum elliotii** Stapf

Sorghum elliotii Stapf in Prain, *Fl. Trop. Afr.* **9**, 118, 1917, is founded on a specimen in Kew Herbarium, *Scott Elliot* 7612, collected in the Toro district of Uganda, near the Ruwenzori Mountains.

DESCRIPTION

An annual or may persist as a short-lived perennial, but basal portion not known. *Culms* slender, up to 1 m. or more high, branched above. *Leaves* small; blades 10–30 cm. long, 8–12 mm. wide, linear, somewhat narrowed towards the base, attenuated upwards and terminating in a narrow pointed apex, dull green, with the somewhat slender mid rib rather prominent below and the margins rough. *Panicle* narrow, sublinear, about 18 cm. long and 2 cm. wide; branches 1–3 from a node, slender, the longer ascending, arching over, subsecund, up to 4 cm. long, bare of spikelets for 1–2·5 cm. from the more or less hairy base, very rough to spinulously ciliate upwards like the branchlets and the rhachis. *Racemes* tough, very tardily disarticulating, few-noded, up to 1·5 cm. long; internodes slender, about 3 mm. long, ciliate with pale fulvous hairs about 1 mm. long; pedicels similar but rather more slender and darker coloured. *Sessile spikelets* ovate to ovate-lanceolate, acute to acuminate, 4·5–5·5 mm. long, 2–2·5 mm. wide, with 4–5 nerves visible between the keels of the lower glume, straw yellow to buff, mahogany red or reddish purple, sparsely strigillose and at length glabrous and shining on the backs of the glumes, awned; callus copiously bearded with fulvous hairs about 1 mm. long. *Glumes* coriaceous but thinner near the tips; lower somewhat rounded in the lower half, 9- to 11-nerved, cross-nerves obscure, keeled from about the middle, with the fine linear margins spinulously ciliolate and merging into the hyaline tip without, or with only obscure, teeth; upper narrowly convex, keeled above the middle and scabrid near the tip, 7-nerved, with fine cross-nerves in the upper half. *Lemmas* finely long-ciliate; lower ovate-elliptic to elliptic-oblong, 4–4·5 mm. long; upper ovate, 3–3·5 mm. long, 2-lobed from 0·5–1 mm. deep, awn 7–13 mm. long. *Anthers* 2–2·5 mm. long. *Grains* broad-elliptic to obovate-elliptic, 2–2·5 mm. long, 1·5–1·8 mm. wide, embryo-mark more or less distinct. *Pedicelled spikelets* 5–6 mm. long, purplish, ♂ or neuter, at length deciduous; lower glume 8- to 9-nerved, upper 7-nerved.

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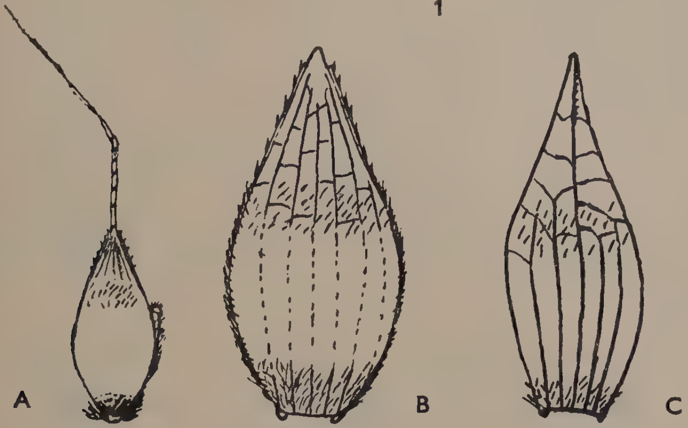

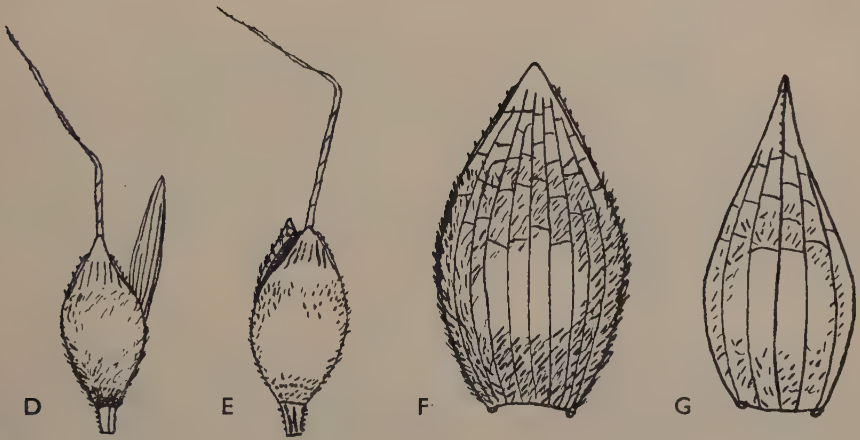

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(1) *Sorghum elliotii* Stapf. A, sessile spikelet and part of pedicel; B, lower glume; C, upper glume, exterior view. (From *Scott-Elliot* 7612.) (2) *S. niloticum* (Stapf ex. Piper) Snowden var. *kavirondense* Snowden; D, sessile and pedicelled spikelets, after flowering; E, sessile spikelet in fruit; F, upper glume; G, lower glume, exterior view. (From *Edwards* 3136.) A, D and E, ×5; B, C, F and G, ×10.

DIAGNOSTIC CHARACTERS AND AFFINITIES

The narrow leaves, 8–12 mm. wide; small narrow panicle; few-noded tough racemes; and the ovate to ovate-lanceolate, acute to acuminate sessile spikelets, 4·5–5·5 mm. long, 2–2·5 mm. wide, with awns 7–13 mm. long, are the distinctive features of this species. It is closely related to *S. verticilliflorum*, but the latter has larger panicles, fragile racemes, and longer elliptic-lanceolate sessile spikelets. *S. elliotii* is also related to *S. niloticum* and *S. castaneum*, but it differs from the former in the smaller panicles and in the shape of the smaller sessile spikelets, as well as in having fewer nerves in the lower glume; and from the latter in its smaller panicles, tough racemes, and longer ovate to ovate-lanceolate, acute to acuminate sessile spikelets.

DISTRIBUTION AND UTILITY

S. elliotii was collected in the Toro district of Uganda near the Ruwenzori Mountains, at a place recorded by Scott Elliot as Kasamaga. It seems possible, however, that this was intended for Kasagama's, for Kasagama was then the Mukama (King) of the Toro district, and he had his capital on a hill near Fort Portal, on the eastern foothills of Ruwenzori. Although this area is much visited by Europeans no further gathering of this species has been made. The tough racemes suggest that it may have originated as a result of cross-fertilization between one of the local grain Sorghums, which belong to *S. caudatum* and *S. nigricans*, and the wild *S. verticilliflorum*, which is common in the district. The basal portion of the plant is missing, and the upper portion has the appearance of a depauperate specimen that may have arisen either from a tiller-shoot or a secondary branch from the upper part of the main stem. This species does not appear to be of any special economic importance for fodder or grazing.

UGANDA. Ruwenzori region, Toro district, at Kasamaga (Kasagama's, Kabarole, near Fort Portal?), on granite, *Scott Elliot*, 7612!

This specimen was referred to by Piper (in *Proc. Biol. Soc. Wash.* **28**, 42, 1915) in a note under his subspecies *Andropogon sorghum niloticus*, but I agree with Stapf that it could not be satisfactorily included in that subspecies although, as already mentioned, it is evidently related to it.

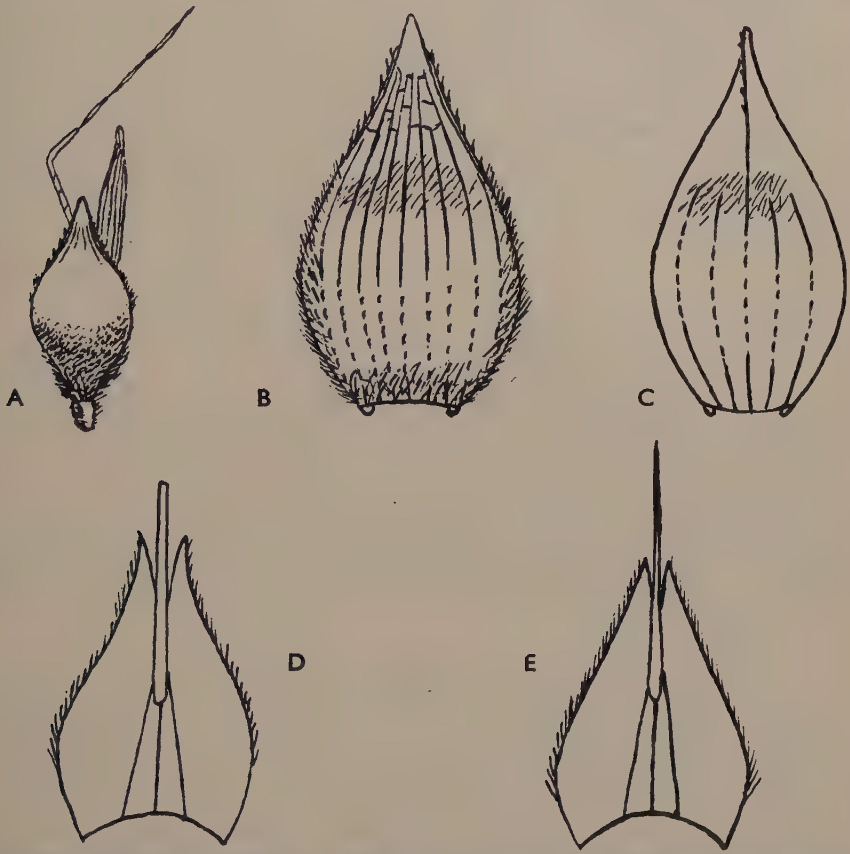
21. **Sorghum niloticum** (Stapf ex Piper) Snowden

Andropogon sorghum (Linn.) Brot. subsp. *niloticus* Stapf ex Piper in *Proc. Biol. Soc. Wash.* **28**, 41, 1915, is based on a specimen in Kew Herbarium collected by Murie (on Consul Petherick's expedition) on the banks of the White Nile, a little south of Gaba Shambe, about 7° N. lat., in the Upper Nile province of the Anglo-Egyptian Sudan.

Sorghum niloticum (Stapf ex Piper) Snowden, stat.nov., is founded on Piper's subspecies *Andropogon sorghum niloticus*, raising it to specific rank on transferring it to the genus *Sorghum*.

DESCRIPTION

A tall annual or loosely tufted perennial about 2·5 m. high. *Culms* rather stout, 4–5 mm. wide at the base of the panicle. *Leaves* many; blades linear, somewhat narrowed towards the base, tapering gradually upwards to the acuminate tip, the uppermost 15–35 cm. long, 1–3 cm. wide, green with some purplish markings, mid rib 1–2 mm. wide and somewhat prominent below in the basal portion, margins spinulously scabrid upwards. *Panicle* loose, oblong to elliptic-oblong, 15–40 cm. long, 8–15 cm. wide; rhachis rather slender, striate and somewhat hairy below, more angular with the ridges scabrid in the upper part; branches one to few from each node, slender and flexuous, soon spreading, the lower 7–15 cm. long, usually naked below for 2–6 cm., more or less hairy at the base and in the angles of the divisions, scabrid upwards like the branchlets. *Racemes* tough, 2- to 6-noded, 0·8–2·5 cm. long, internodes and pedicels slender to rather slender, 1·5–3 mm. long, densely ciliate with fulvous or tawny to ferruginous hairs about 1 mm. long. *Sessile spikelets* elliptic-ovate to elliptic-rotund, acute to acuminate with the tips closed, or subacute with the tips slightly open, 4·5–6 mm. long, 2–3 mm. wide, straw yellow to deep cream or tawny with 5–6 greenish nerves visible between the keels of the lower glume when young, at length often mahogany red to maroon, chocolate brown or almost black, sparsely strigose at the base, sides, and just above the middle, otherwise glabrous and shining, awned or with a short bristle; callus densely bearded when young, sparsely at maturity. *Glumes* firmly coriaceous but with rather thinner tips; lower slightly rounded on the back, 11- to 13-nerved, finely 2-keeled in the upper third, scarcely or obscurely margined, usually with the keels merging gently into the hyaline tip but sometimes ending in minute teeth; upper narrowly convex, usually 7-nerved, scabrid on the sharp keel in the upper fourth. *Lemmas* thinly to moderately ciliate; lower elliptic-ovate, 3–4·5 mm. long, 2-nerved, or rarely 3-nerved and then acuminate to mucronate; upper ovate, 3–4 mm. long, 1- to 3-nerved, 2-lobed to a depth of 0·5–1 mm. and with an awn 8–12 mm. long, or sometimes with a bristle 2–5 mm. long. *Anthers* 2·5–3 mm. long. *Grains* obovate-elliptic to obovate, 3–4 mm. long, 1·5–2·5 mm. wide, dark brown; embryo-mark distinct. *Pedicelled spikelets* at length deciduous, 3·5–6 mm. long, mostly neuter, often purplish; lower glume 8- to 11-nerved, upper 5- to 7-nerved; anthers 0 or up to 2·8 mm. long.



Sorghum niloticum (Stapf ex Piper) var. *niloticum*. A, sessile and pedicelled spikelets; B, lower glume; C, upper glume, exterior view; D, upper lemma of awned spikelet, with basal part of awn; E, upper lemma with bristle. (All from *Murie*, banks of the White Nile.) A, × 5; B–E, × 10.

DIAGNOSTIC CHARACTERS AND AFFINITIES

S. niloticum is distinguished by the long narrow leaves; moderately large but narrow loose panicle; tough racemes; and the elliptic-ovate to elliptic-rotund, acute to acuminate and closed, or sometimes subacute and slightly open, sessile spikelets 4·5–6 mm. long, and 2–3 mm. wide. It differs from the related *S. elliotii* in the larger panicles and the broader elliptic-ovate to elliptic-rotund sessile spikelets, as well as in having larger grains when mature. It is also related to *S. castaneum* and *S. verticilliflorum*, but it may be separated from both by the tough racemes as well as from the former by the larger sessile spikelets and from the latter by the broader elliptic-ovate to elliptic-rotund sessile spikelets.

Distribution and utility

Up to the present this species has been recorded from the Upper Nile and Mongalla provinces of the Anglo-Egyptian Sudan, the Chua district of northern Uganda, the Kavirondo province of western Kenya, and the eastern part of the Belgian Congo. It has the appearance of being equal to *S. verticilliflorum* as a fodder crop, with the additional advantage of having larger grains and tougher racemes, which latter should facilitate the harvesting of the seed. It does not appear to have been much used for feeding stock, however, although the variety *kavirondense*, described below, is now under trial as a fodder crop in Kenya Colony. Most of the specimens enumerated below have been found on grasslands following after cultivated lands have been abandoned and allowed to become overgrown.

(i) Var. **niloticum**

Var. **niloticum**, based on *Sorghum niloticum* (Stapf ex Piper) Snowden.

Sessile spikelets elliptic-rotund, acute to acuminate, 5–6 mm. long, 2–3 mm. wide, awned or sometimes with a short bristle; grains 3–4 mm. long, 1·5–2 mm. wide, completely hidden and enclosed by the glumes when mature.

This variety is based on the specimen collected by Murie in the Anglo-Egyptian Sudan, which is also the type of the species.

Belgian Congo. Bokola, *Vanderyst* 1540!

Anglo-Egyptian Sudan. Upper Nile Province, on the banks of the White Nile, south of Gaba Shambe, *Murie*! Mongalla province, Nimule and Rejaf, *Shantz* 897! 945! *Shantz* 898! Also from Nimule, Mongalla province, is somewhat intermediate between this variety and *Sorghum castaneum*.

(ii) Var. **kavirondense** Snowden

Var. **kavirondense** Snowden, var.nov.; Spiculae sessiles elliptico-ovatae, acutae vel subacutae, 4·5–5·5 mm. longae, 2–2·5 mm. latae, aristatae; caryopsides 3–3·5 mm. longae, 2–2·5 mm. latae, inter glumas inclusae vel maturae inter glumas arcte appressas leviter apertae.

Sessile spikelets elliptic-ovate, acute or subacute, 4·5–5·5 mm. long, 2·5–3 mm. wide, awned; grains 3–3·5 mm. long, 2–2·5 mm. wide, enclosed by the glumes or when mature slightly exposed between their closely appressed tips.

This variety is founded on a specimen collected in the Kavirondo province of western Kenya, *Edwards* 3136, which is in Kew Herbarium.

Uganda. Chua district, ex *U.S. Dep. Agric. Sorghum Herb. F.C.I.* 8681!

These two specimens have leaves 5–6 cm. wide, which may be due to cultural conditions.

Kenya Colony. Kavirondo province, near Maseno, *Edwards* 3136!

Stapf (in Prain, *Fl. Trop. Afr.* 9, 118, 1917) referred to Murie's specimen in a note under *S. verticilliflorum*. He expressed the opinion that it was probably a state of the latter species with the sessile spikelets bulging more than usual and with rather tardily disarticulating racemes. The shape of the sessile spikelets, however, which are wide in proportion to their length, differs from that of *S. verticilliflorum*, and the grains are usually larger and wider than those of that species. After examining the additional material received at Kew since Stapf's account of the African Sorghums was published, I have come to the conclusion that Murie's specimen belongs to a separate species related to, but much less common than, *S. verticilliflorum*, at present restricted to a limited area near the White Nile and the adjacent African Lakes Region.

Notes on the alga Compsopogon Mont. By F. R. Jones, B.Sc. (Chelsea Polytechnic)

(With 15 Text-figures)

[Read 6 May 1954]

Compsopogon (Rhodophyceae) is restricted to tropical and subtropical regions, and cannot normally survive in temperate areas. Species occur in North and Central America, Africa and India, *C. corinaldi* Kuetz from Italy being the only European representative. *C. leptoclados* Mont., native of Guiana, has been recorded from the Reddish Canal, Manchester, where the waters are heated by influx of hot water from cotton mills. Here the alga was restricted to a temperature range of 23–24° C. *Compsopogon*, however, occasionally appears and flourishes in tropical fish tanks where the water temperature is generally maintained at about 24° C.; such an occurrence was the source of the material for this study.

Fritsch has provisionally placed *Compsopogon* with the Bangiales. The genus is small; about seven or eight of the forms described are perhaps good species, and though similar in general form and habit, are for the most part readily distinguished on microscopic examination.

They form richly branched filamentous growths, bushy in appearance and generally attached by a small holdfast. In the older parts of the plant the cells of the uniseriate filaments enlarge and become corticated by peripheral segmentation.

Sporangia of two types, distinguished by Thaxter as macrosporangia and microsporangia, occur, and both appear to function asexually only. They arise sporadically from any cell of the cortex or filament. A dividing wall appears in the mother cell. The inner derivative remains vegetative; the outer develops directly into a macrosporangium, or divides repeatedly to form a group of small microsporangia which come to lie on the surface of the thallus. The spores, non-motile and naked, are produced singly from the entire contents of each sporangium.

The macrospores may be regarded as homologous with the monospores produced by diverse Bangiales. Thaxter succeeded in germinating them but did not follow their development. A sexual significance has been attached to the microspores, and though this possibility has not been ruled out, it seems likely that their function is asexual. They resemble the macrospores closely, except in size. Skuja considered that microspores formed the usual method of reproduction and that macrospores were formed in response to artificial cultural conditions, but this view does not receive support from the present investigation.

METHODS

Material for the investigation was grown in heated aquaria with water capacities ranging from 5 to 20 gallons, and maintained at 24–27° C. One tank received only artificial illumination, the others depended entirely on natural daylight.

For daily observations on growth complete small plants attached to pieces of *Vallisneria* leaf and mounted between slide and cover-slip were employed. The cover-slip was supported on strands of thread and held in place by rubber bands. The slides could then be immersed in the tank and removed for observation at any time without damage. Attempts to grow the alga in closed systems, placing it in nutrient solutions in hanging-drop cultures and cavity slides, were not successful.

Most of the observations were made on living material, but double stained whole mounts were also prepared and proved useful for confirmatory purposes. Sections from 6 to 15 μ were also cut of wax-embedded material. All permanent preparations were stained with Heidenhain's haematoxylin and counterstained with fast green. The fixative employed was form-acetic-alcohol, which gave satisfactory results.

The species to be described has been identified as *Compsopogon leptoclados* Mont. by comparison with preserved material in the British Museum (Natural History), South Kensington. When grown in a tank with good illumination it attains a length of 7–9 cm., forming a somewhat coarse growth of blue-green filaments. The main axis may be unbranched or may bear up to twenty or more branches borne laterally in one plane. Some of the primary branches may branch again but rarely more than once or twice. The young filaments are uniseriate; farther away from the apex in the older plant, the cells of the filament enlarge and cut off peripheral segments to form a one-layered cortex. The basal part of the axis, however, does not become corticated, but produces numerous septate rhizoids which form a small but compact holdfast 2–3 mm. across.

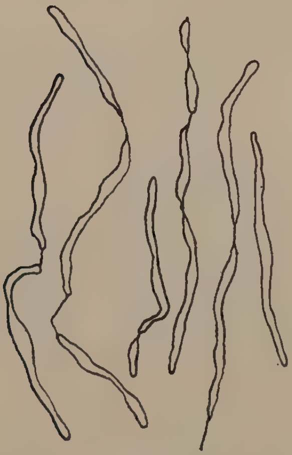


Fig. 1.

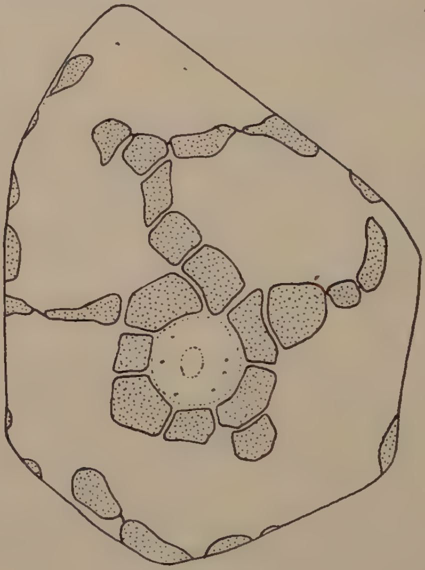


Fig. 2.

Fig. 1. Thread-like chloroplasts from enlarged axial cells. × 2000.

Fig. 2. General appearance of cell soon after spore production. No starch. Nucleus here adjacent to cell wall. × 2000.

THE CELL

The cell wall appears to be composed entirely of pectic substances. It stains deeply with methylene blue, but is not soluble in boiling water. Cellulose dyes—azo-blue, congo-red and Schultze's solution—have no effect; iodine stains only the cell contents.

The chromatophores are parietal; they vary in size, shape and abundance from cell to cell. In the spore they are small, crowded and approximately discoid (Fig. 5), while in the enlarged cells forming the axial series of the older filament they are fine, thread-like and widely spaced (Fig. 1). These two conditions form the extremes between which all intermediate forms are found.

In the cortical cells the ribbon-like, irregularly lobed chloroplasts are larger and more closely fitted on the side of the cell towards the exterior, whereas adjacent to the enlarged axial cells they are comparatively small and widely spaced.

The chloroplasts are normally blue-green in colour. They appear to grow in length continuously; occasional constrictions appear and deepen and the two parts separate, remaining connected by a fine thread (Fig. 3). No pyrenoids occur.

Floridean starch is found in nearly every cell. The grains are approximately ovoid and range in length from 0·5 to an extreme of 0·7 μ. They stain slowly with iodine; pale brown at first, gradually increasing in intensity to a very dark brown. Usually they lie free in the cytoplasm; occasionally in contact with a chloroplast but never embedded in its substance. They form a loose sheath around the nucleus, each grain in contact with the nucleus but clearly separated from its neighbours. This sheath persists after all other grains have disappeared from the cell; very seldom is it entirely absent though occasionally it consists of only a few grains. Perhaps the nucleus is especially concerned in the formation of these grains, as is probably the pyrenoid in some Chlorophyceae.

The nucleus is comparatively large, with an average diameter of 6–7 μ. It lies immediately internal to the cell wall, when the chloroplasts often form a loose sheath round it (Fig. 2). The prominent nucleolus, reaching up to a third or even a half of the diameter of the nucleus, may readily be seen in living material. The nucleolus alone appears to pick up stains; the rest of the nucleus, devoid of chromatin, is most readily delimited by observing the starch sheath. Apart from the nucleolus, no other structure has been observed in the nucleus; at times of cell division the nucleus has always been obscured by starch grains or chloroplasts. Serial microtome sections revealed no further structure or evidence of mitosis.

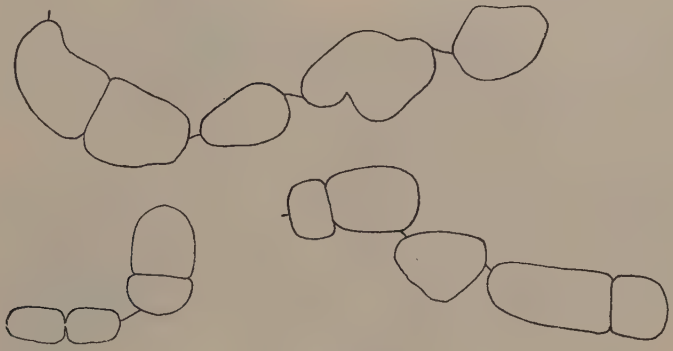


Fig. 3. Stages in chloroplast division.

SPORANGIUM DEVELOPMENT

Reproduction is by means of large, naked, non-motile monospores, produced singly in sporangia. Thaxter refers to these as macrospores.

Sporangia may develop from any of the cells of the cortex or of the non-corticated filament, including the terminal cell. Production of sporangia may continue vigorously in the same plant for 6–8 weeks, when frequently up to 20 % of the surface cells of the plant may be so engaged at any one time. Sporangium development generally begins soon after cortication has begun in the lower parts of the plant, though at first only a few scattered cells are involved. The whole sequence, from initiation of sporangium formation to expulsion of the spore, occupies 2 or 3 days depending on light intensity, the shorter time when conditions are optimum with bright sunny weather.

The first indication of sporangium formation is an increased denseness in the cell concerned; this appearance is due to an increase in chloroplast area and to a greater increase in the number of starch grains (Fig. 4*a*). To one side of the cell the wall bulges out, and in this region the accumulation concentrates. In the early stages the chloroplasts break up into short segments, approximately isodiametric, and in some material they can be seen joined in series by short fine threads. When the chloroplasts of the mother cell are ribbon-like they often converge in rows on the dense region, chloroplast segments constricting off at their ends. Later the great accumulation of starch round the outer region of the developing sporangium hinders observations on the chloroplasts. Much of the starch in the less dense side of the mother cell eventually disappears, and a wall is laid down separating the dense sporangium from a now apparently normal sister cell. Observations on the nucleus during this period are difficult.

Soon after the sporangium has been cut off the mother cell, a clear area appears immediately below the apex of the bulge in the outer wall, the bulge itself now being quite prominent. The sporangium at this time appears very dense and spore discharge is imminent (Fig. 4*b*). It stains readily with iodine due to the great accumulation of starch. The actual discharge of the spore has been fully described by Thaxter; suffice it to say that the sporangium wall, above the clear area of the spore, ruptures, and the naked spore quickly squeezes out, assisted by the pressure of the cell below. Expulsion is not very violent and the velocity of discharge is only sufficient for the spore to become clear of the parent filament.

Immediately after discharge the sister cell pushes up the septum, which had separated it from the sporangium, and very quickly almost fills the empty space. Complete filling takes a little longer. This cell is now 'diluted'; the contents appear unusually clear on account of the comparatively few starch grains and the well separated chloroplasts. After a rest of several days the process may be repeated, another sporangium being formed by the same mother cell. Developing (Fig. 4*a*) or mature sporangia have frequently been noted with the remains of the previous sporangium still attached. No direct or inferred evidence has been obtained of a repetition for a third time.

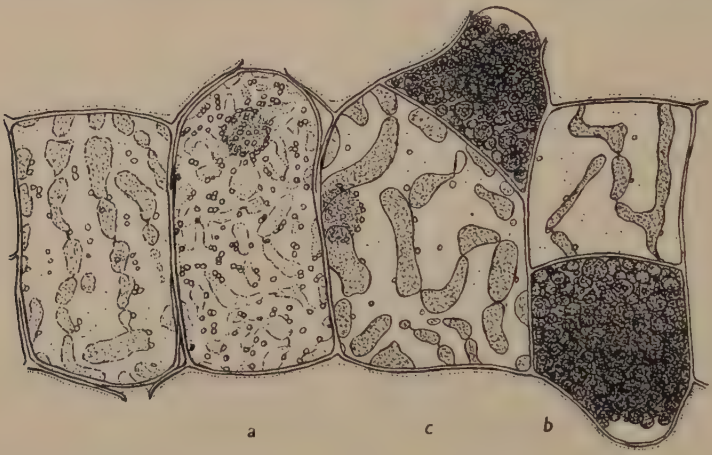


Fig. 4. Sporangia: (*a*) chloroplasts are multiplying and starch accumulating; (*b*) sporangium mature; (*c*) commencement of liberation of spore. × 800.

Spore discharge occurs readily on transferring a piece of material to a slide, but after 2 or 3 min. all discharge ceases and will not start again if disturbed till more sporangia are ripe.

SPORE GERMINATION AND DEVELOPMENT

The spore on discharge (Fig. 5) is spherical, 19–20 μ across, and naked. There is no vacuole. The large central nucleus with a diameter approximately one-third of that of the spore, is generally discernible. Many discoid or oval chloroplasts and numerous starch grains are scattered throughout the spore. Germination occurs only when in contact with a suitable substratum—lodged in the toothed notches of *Vallisneria* leaves, or retained on flat rough stones—otherwise they disorganize within a day. Attempts to obtain germination in hanging-drop culture were not successful, but germination was induced by mounting spores with *Vallisneria* leaf between slide and supported cover-slip, the whole being immersed in the aquarium.

Shortly after discharge, and generally before attachment, vacuolation of the spore begins (Fig. 6); three to six or more vacuoles become evident, starch grains outlining their surfaces (so that in size and form they appear superficially like nuclei) with frequently one or two larger starch grains from 1·5 to 1·7 μ across in Brownian movement within. By the time attachment has been accomplished, vacuolation is complete with the nucleus and chloroplasts now peripheral and a slight decrease in the amount of starch.

The spore flattens against the substratum and becomes walled. Growth is slow at first and after 2 days the spore often shows an irregular outline though an oval shape is more usual. The first two divisions are almost simultaneous, separating off two small cells from a larger central cell from which the erect system will arise. The smaller cells give rise to the prostrate system. They grow out over the substratum as much-branched filaments and eventually form a compact one-layered expanse. Growth is apical and branches originate as lateral bulges on subterminal cells (Figs. 8, 9). The cells are similar to those of the erect filament but are smaller and tend to be greater in length than in breadth. The chloroplasts are irregular but approximately isodiametric.

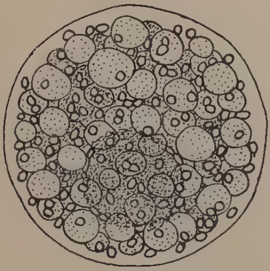


Fig. 5.

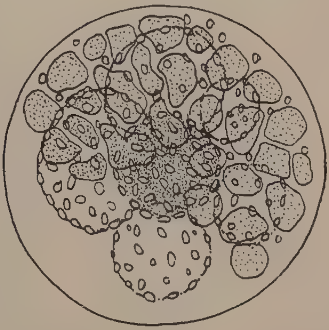


Fig. 6.

Fig. 5. Macro-spore immediately after expulsion from sporangium. × 1600.

Fig. 6. Vacuolation of spore (chloroplasts and starch grains omitted on one side). × 2000.

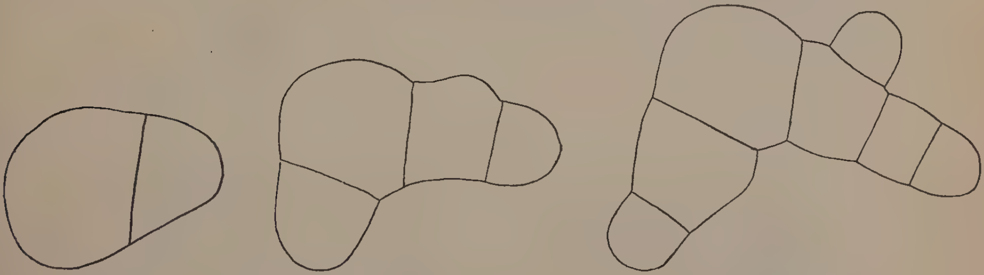


Fig. 7. Fig. 8. Fig. 9.

Figs. 7–9. Successive stages in development of prostrate system; drawn from one spore at daily intervals. × 1000.

Initiation of the first erect filament begins when five or more cells are present. A prominent bulge appears on the upperside of the central (original) cell and this region appears dense from an accumulation of starch and large numbers of small peripheral chloroplasts. As the bulge increases, a protoplasmic bridge appears in the position of the future separating wall, with the nucleus embedded in its central region. Later when the septum is complete the nucleus in the upper cell—the first cell of the erect filament—migrates to the apical end where it lies close to the wall; this occurs after every division in the terminal cells of both erect and prostrate systems (Fig. 10). The apical cells always present the same appearance; the free terminal end containing the nucleus, abundant starch and crowded, small, multiplying chloroplasts, gradually grading to the more mature condition in the lower part of the cell, cross-walls appearing here as this latter region extends. Subsequently one or more further erect threads may arise from neighbouring cells of the prostrate cushion though typically only one main axis develops.

If the spore develops on other than a solid substratum, such as a tangle of *Leptothrix* threads, development is different. The spore becomes walled as usual but does not develop an irregular outline. It becomes oval and grows out from the thinner end; growth occurs only on this side and the cells cut off are long—several times longer than broad—and sinuous, with elongated ribbon-like chloroplasts (Fig. 11). The whole resembles the later formed rhizoids of the mature plant in appearance. Development in such cases never appears to get far; a long filament (though of few cells) may result but never more has been observed.

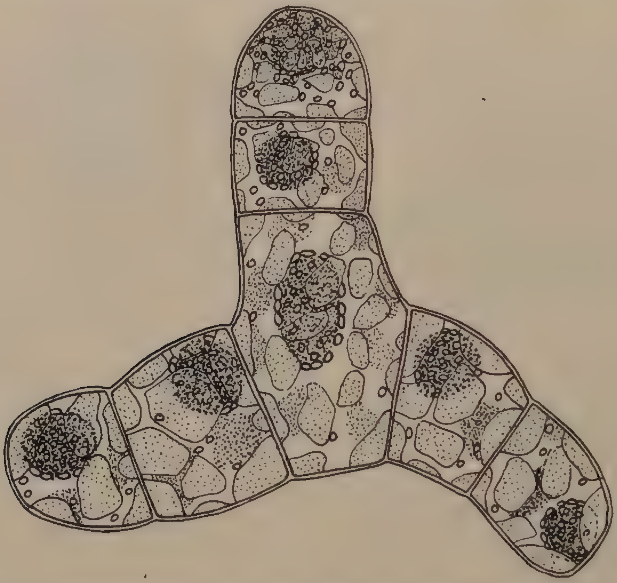


Fig. 10. Young sporeling from side, with early erect filament (*e*). × 1600.

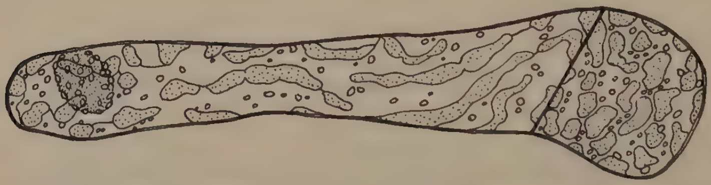


Fig. 11. Form of sporeling when on a loose substratum. × 1000.

DEVELOPMENT OF THE MATURE PLANT

Soon after initiation of the erect filament, growth becomes rapid. Growth is both apical and intercalary. The cells cut off from the dome-shaped apical cell commonly divide twice and occasionally 3 times before division ceases. The young cells are short, the breadth (13–14 μ) being about twice the length. At first, growth is longitudinal only but shortness is maintained by transverse division. When division has ceased the breadth increases steadily with a slower increase in length till the cells near the base of the plant are about 40 μ wide. The same general shape is retained throughout this increase in size from the apex back, with the width of the cells about 2½ times the length. The widest region of the filament occurs about 7–10 cells up from the base and from here downwards the diameter decreases progressively to the lowest cell which retains its original size, so the filament at its base tapers out as an inverted cone to the attaching prostrate system.

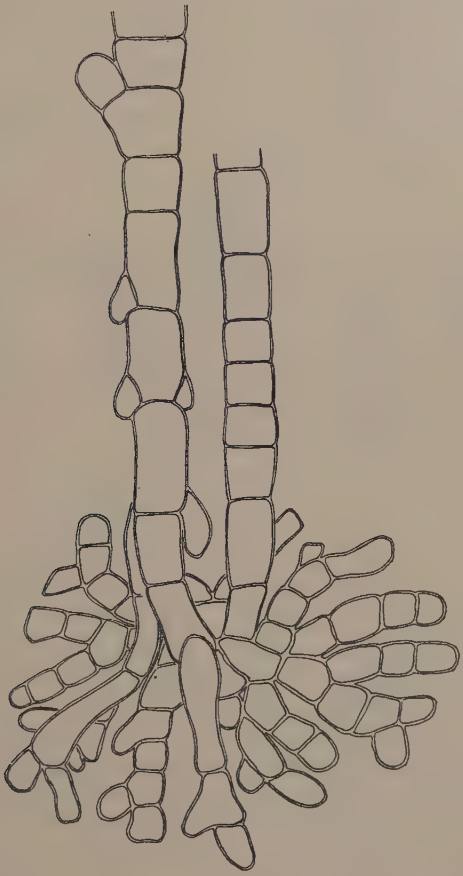


Fig. 12.

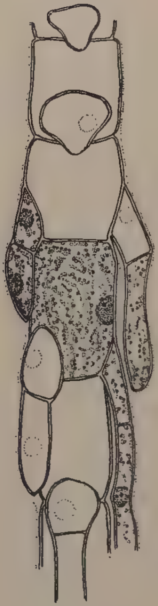


Fig. 13.

Fig. 12. Young plant, prostrate system well developed; rhizoids in several stages of development, and one lateral branch initial. × 500.

Fig. 13. Developing rhizoids. × 500.

The plant is now about 2 mm. long and consists of a filament of 160–180 cells. The prostrate system (Fig. 12) has continued to grow slowly, fanning out over the substratum. Rhizoids (Figs 12, 13) now begin to develop from the lower ends of the basal cells of the erect filament, appearing first as small, downwardly directed bulges in which the protoplast appears slightly more dense from accumulation of starch grains. The rhizoid initial is cut off by an oblique wall which reaches the lower cross-wall of the mother cell about one-third of its diameter from the outside. Consequently these lower axial cells now appear truncated at their base. The rhizoids commonly appear in pairs, one either side of the cell, with each pair at right angles to the pair above and below. The rhizoids are long narrow cells with elongated chloroplasts. They grow down the main axis closely appressed to its surface and grow and branch over the prostrate system. Further rhizoids later arise from other regions of the same axial cells and from the upper cells of the earlier formed rhizoids.

Cortication commences soon after the appearance of the first rhizoids; tangential walls appear sporadically in the lower broader regions of the filament (apart from the basal ten or so cells engaged in rhizoid production) cutting off peripheral segments, followed later by further divisions to separate off a complete cortex from a central axial cell. Sometimes before, sometimes after this beginning of cortication, the branch initials (Fig. 14) appear. A bulge appears at the upper end of an axial cell and turns sharply upwards. The contents are dense—many small chloroplasts and starch grains—and the projection is cut off by a wall which lies outside the plane of the outer walls of the filament. Growth of the initial continues as in the main axis. The lower branches are spaced about 15–20 cells apart but the spacing becomes greater (up to 40–50 cells) towards the apex of the plant. Branches are cut off on two sides only so that all lie in one plane; a mature plant may bear up to twenty but some plants do not branch at all, consisting only of a single stout filament. Branch and rhizoid initials differ from sporangia in the position of the cross-wall, being less dense, restricted to one end of the side of the cell and lacking the clear region opposite the bulge.

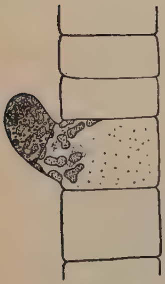


Fig. 14.

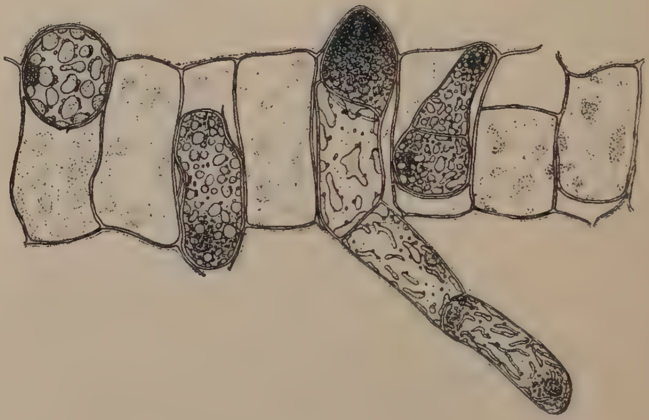


Fig. 15.

Fig. 14. Branch initial. × 500.

Fig. 15. Spores developing *in situ* in dead filament. × 500.

After cortication the central axial cells do not divide further but grow steadily in length and diameter, the cortical cells dividing occasionally in all directions to keep pace with this enlargement. Also, as a consequence the lateral branches become well spaced. In a plant 35 mm. long the axial cells near the base were 145 μ broad and 85 μ long. The lower ten or so axial cells lengthen to the same extent but do not increase much in breadth, resulting in an exaggeration of the inverted cone base to the filament but hidden by the overgrowing mass of rhizoids which are now being produced also by the lower cells of the cortex. In this species the cortex remains one-layered. The primary branches may produce one or two secondary branches. In a large plant the apices of the main and primary branches have generally ceased growing and are frequently dead or broken off. Hence most of the growth of the plant by means of cell-division has ceased by the time cortication is well under way and the subsequent increase in size is almost entirely the result of the great extension of the central axial series of cells.

In old plants (8–12 weeks) various abnormalities occur. By this time they are generally thickly covered with epiphytic growths of algae and bacteria. Parts of the plant may die, perhaps resulting from injury, but isolated cells (Fig. 15) may remain healthy and green and these appear to be identical in position, shape and contents to sporangia. In most instances observed the contents develop a separate wall inside the sporangium and germinate at one or other end to form a string of long, narrow, twisting cells resembling a rhizoid. No specimen observed ever got further than a few-celled filament before becoming invaded by bacteria, but perhaps in a natural habitat of running water further development might occur.

When the main or a lateral axis is broken at any position in the corticated region, the cortical cells near the point of injury produce septate sinuous rhizoid-like outgrowths similar in appearance and fate to those of spores germinating in sporangia or on a loose substratum. Similarly, if a branch is cut off, the enlarged axial cell below may grow up like a massive rhizoid.

Sometimes the terminal non-corticated filaments show an unusual appearance resembling hormogone formation in the Cyanophyceae. Every fifth, sixth or so cell appears biconcave, with chloroplast axile and homogenous. These cells are dead, the shrunken protoplast being separated from the cell wall by a homogenous fluid giving the appearance, on a cursory examination, of a thick wall. Large quantities of Floridean starch are contained within the shrunken protoplast as shown by iodine staining. There is no tendency for the filaments to break at these points; the normal cells on either side simply bulge into them till the squashed dead cell appears as a layer of cement substance between them. On occasions rows of a dozen or more such dead cells have been noticed; then the terminal normal cell below them grows up and through the dead cells, the dead protoplasts being pierced and forming a collar around the new filament. Dead cells generally assume a pink or blue colour.

Adventitious branches are also frequent in old senescent plants, arising from cortical cells. They rarely develop to more than 20 cells and remain narrow and uncorticated. There is no reason to link these with anomalous development of sporangia.

In very old senescent plants all co-ordination between cells appears to be lost. Each cell, of the cortex or non-corticated filament, grows irregularly and bulges on either side, giving the plant a very knobbly appearance under the lens.

The principal factors influencing the size and form attained in the aquarium are temperature and light. Above 20° C. the plant is able to maintain itself, but for optimum growth a temperature of 24–26° C. is required. Ideal illumination is provided by direct summer daylight or by a 40 W. electric light bulb burning 8 hr. daily and within 15 cm. of the plant. Under conditions of low light intensities the plants rarely reach more than 2–3 mm. in length and remain as simple filaments or with only slight indications of cortication. Such plants have been kept for over 6 months, growing very slowly, but still producing small numbers of spores which colonize more favourable situations. With natural lighting, the large plants break up and disappear during October and November, but these dwarfed plants survive, generally on more permanent situations such as large rough stones, to provide a nucleus for re-colonization the following spring.

The degree of branching is correlated with the density of the plant populations; isolated plants generally bear twenty or more primary branches, but plants growing from a close mat of sporelings remain as simple unbranched growths though otherwise normal in length and structure.

Microsporangia were at no time observed in any material.

SUMMARY

The development of *Compsopogon leptoclados* Mont. from the spore to the mature plant is described.

ACKNOWLEDGEMENTS

The writer wishes to express his gratitude to Dr B. Barnes for his advice and interest during the progress of the work, and to Dr H. Duerden, who suggested the investigation, for several useful discussions.

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On the occurrence of secondary thickening in palaeozoic ferns. By H. S. Holden.

(With Plates **16** and **17**, and 5 Text-figures)

[Read 21 April 1955]

The development of secondary thickening in palaeozoic ferns presents a number of puzzling and unexpected features. At one extreme we have nothing beyond the production of a localized cambium, whilst at the other there is the development of a well-marked zone of secondary xylem, often of considerable thickness involving both root and stem. Between these two extremes there occur a number of types in which secondary thickening is confined to one organ, stem or root, in either of which it may be scanty in amount or well developed. In other cases in which, normally, no secondary xylem occurs, it may develop as a traumatic response. In some examples of this type of response the evidence is unequivocal but in others, owing to the imperfect preservation of the material, we have to rely on the distribution and character of the secondary elements and on a comparison between the appearance of the organs in which they occur and those which are normal for the species. Quite apart from the species in which secondary thickening is either a constant feature or is either probably or certainly due to wounding there are isolated examples in which, though neither stem nor root normally show any indication of cambial activity, a single root or other organ may, from some unexplained cause, produce an appreciable amount of secondary xylem.

The development of secondary xylem in both stem and root as far as is known is characteristic of only two palaeozoic ferns namely *Botrychioxylon paradoxum* and *Zygopteris primaria*. We owe our detailed information with regard to these two fossils to Scott (1912) and Sahni (1932*a*) respectively. Both plants are characterized by the xylem of the stem stele possessing a stellate central core of mixed tracheids and parenchyma surrounded by a broad zone of secondary xylem showing typical seriation of the tracheids. The leaf traces in both ultimately assume the anatomical features of Bertrand's petiole genus *Etapteris* (Bertrand, 1909) and it is possible, as Sahni has suggested, that had the close resemblances between *Botrychioxylon* and *Zygopteris primaria* been known prior to the publication of his detailed study of the latter species the establishment both of the genus *Botrychioxylon* and of the petiole genus *Etapteris* might have been unnecessary. In our present state of knowledge, however, their retention is probably fully justified. It is a point of some interest that whilst in the petiole itself the vascular supply in these two plants consists wholly of primary tracheids these are replaced, at and near their point of origin, very largely by elements of secondary origin. Many of the normally diarch roots also show secondary thickening, most of the constituent tracheids in *Zygopteris primaria* being of a somewhat larger diameter than those of the stem. In this plant the secondary tracheids form two broad, wedge-shaped groups, the narrowed bases of which adjoin the metaxylem of the diarch plate (Text-fig. 1). The tissue lying between the two wedge-shaped groups and which overarched the protoxylem poles consisted, it is reasonable to suppose, of secondarily produced parenchyma though this, unfortunately, has not been preserved. In the roots of *Botrychioxylon* the secondary tracheids appear, judging from the best-preserved specimens, to have completely enclosed the primary diarch plate apart from a comparatively narrow ray opposite the protoxylem groups, and Text-fig. 2 is a camera lucida sketch from slide no. 2466 in the Scott Collection illustrating this condition.

In *Ankyropteris corrugata* we have an example of a species in which secondary thickening is normally restricted to one organ, the root. This possesses a stout diarch xylem plate similar in type to that characteristic of the Osmundaceae. In some of the larger roots the primary tracheids are augmented by a wide arc of secondary elements developed on either side of the primary tracheidal group. Exceptionally, as in the root figured in Pl. **16**, fig. 1, the arcs of secondary xylem are interrupted opposite both the protoxylems by a broad strip of secondary parenchyma thus recalling the condition occurring in *Zygopteris primaria*. More commonly these polar strips of parenchyma are much smaller in extent (Pl. **16**, fig. 2), as in *Botrychioxylon paradoxum*, and in some roots are replaced by short, somewhat stumpy tracheids so that a continuous cylinder of secondary xylem results. An example of this condition is shown in fig. 3 of Pl. **16**, and other examples are well shown in roots present in the slides numbered 2685 and 2721 of the Scott Collection.

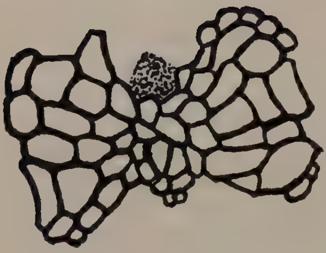

Fig. 1.

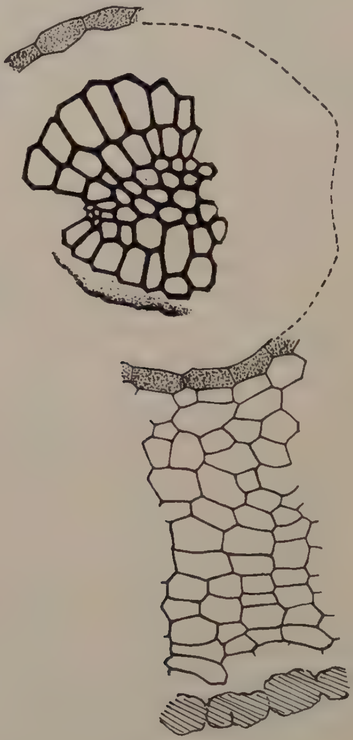

Fig. 2.

Text-fig. 1. Transverse section of the stele of a root of *Zygopteris primaria* showing the characteristic type of secondary thickening. × 63. After Sahni (slightly modified).

Text-fig. 2. Transverse section of a root of *Botrychioxylon paradoxum* showing the stele and part of the cortex. × 90. (Scott Coll. 2466.)

Although secondary thickening is normally confined to the root in *Ankyropteris corrugata*, it may be developed as a traumatic response in both stem and petiole. Before describing examples of these wound reactions, however, it will be convenient to describe a further example of a root in which secondary thickening occurs although, as yet, we do not know of what plant these roots formed a part. The specimens, which were discovered by the late James Lomax in a nodule from Shore, occur in slides 3110 to 3119 in the Scott Collection. There are, however, in addition to these, two further slides numbered J 24 and J 25, cut from the same block, in the University College (London) Collection. These slides are all labelled '*Botryopteris* sp.nov.' but, in my opinion, the correctness of their assignation to the genus *Botryopteris* is extremely doubtful, an opinion which, I understand, is shared by Dr Sergius Mamay of the U.S. Geological Survey, who has also examined the relevant slides in the Scott Collection. There appear to be somewhat sounder grounds for assigning them to an as yet unidentified zygopterid since all the ferns of this group of which the root structure is known (e.g. *Ankyropteris corrugata*, *A. grayi*, *Diplolabis römeri*, *Metaclepsydropsis duplex*, *Austroclepsis* (*Clepsydropsis*) *australis*) are characterized by roots with a similar stout bipolar xylem plate, a feature which appears to be almost exclusively found in this group of palaeozoic ferns. Every stage in the growth of these roots is represented in the slides examined, from one in which the metaxylem of the primary diarch plate is still in part immature (Pl. **16**, fig. 4) to one in which secondary thickening is well developed. One of the most distinctive features of this root is the character of the surface layer, this consisting of closely set digitate or papilliform thin-walled cells (Pl. **16**, figs. 4–6). The secondary tracheids, where these are developed, form two wedge-shaped masses in the plane at right angles to the protoxylem poles thus recalling the condition found in *Zygopteris primaria* but, whilst in the latter the primary and secondary xylem alone are preserved, in the root now described the preservation of the parenchymatous tissues is frequently exceptionally good. Pl. **16**, fig. 5, is a photomicrograph of a transverse section of one such root which shows, on the upper side of the figure, both cambiform cells and an immature, flat secondary tracheid. The same figure shows the development of the periderm in the more superficial layers of the cortex a feature which recalls the formation of the same tissue in the larger roots of *Ankyropteris corrugata* (cf. Pl. **16**, fig. 2). It will be seen from the longitudinal section (Pl. **16**, fig. 6) that not only the outer layers of the cortex but also the digitate superficial cells are involved in the cell-divisions which give rise to the periderm.

Our knowledge of the process of secondary thickening in roots has been largely built on the detailed investigations made by Van Tieghem, whose work was published over eighty years ago (Van Tieghem, 1870). He established the fact that secondary thickening in all roots in which it occurs is initiated in the conjunctive parenchyma lying between the centre of the metaxylem and the phloem. With increase in the age of the root the cambium arches over the protoxylem poles and forms a continuous layer as a result of divisions in the pericycle. In those cases in which secondary activity leads to the production of xylem elements on the whole of the inner face of the cambial layer a continuous cylinder of secondary xylem results, but Van Tieghem gives a number of examples of both diarch and polyarch roots in which the cambial products opposite the protoxylem poles consist entirely of secondary parenchyma. This secondary parenchyma forms broad rays and generally gives a fan-shaped outline to the groups of secondary xylem as seen in transverse section. The examples Van Tieghem described are quoted by De Bary (1884), who also records additional cases in one of which, a diarch adventitious root of *Urtica dioica*, the secondary xylem forms an almost flat bifacial plate in the plane at right angles to that of the protoxylems.

In contrast to the condition characterizing the root of *Ankyropteris corrugata* neither the stem nor petiole of this species normally develops any secondary tissues. There are however, two examples known of stems in which cambial activity not due to wounding, has been found to occur. In one of these, which occurs in the classical specimen originally described by Williamson (1877), what appears to be undoubted secondary thickening is developed at one pole at the base of an outgoing leaf trace (Pl. **16**, fig. 7). One of the sections showing the feature was figured by Williamson (1877, pl. V, fig. 19) who, however, makes no mention of its exceptional character. It had, nevertheless, been noted by the late Dr D. H. Scott who, in his manuscript notes on the Williamson slide, writes: ‘On the S. side of the leaf trace is a mass of...short tracheids with a secondary look evidently the base of some appendage.’ The short tracheids to which Scott's note refers show a well-marked radial arrangement, and though the section is a thick one cambial cells can be quite readily detected in places along their outer margin. The thickness of the section offered insuperable difficulties on attempting to obtain a photomicrograph, and it was decided to try the next slide in the series and here Scott's notes proved of great help for he had shown Williamson's seriation and numbering of slides 245–250 to be incorrect, the slide numbered 248 being the *first* in the series and slide no. 245 being the *fourth*. The photomicrograph forming fig. 7 in Pl. **16**, which is from slide no. 245, shows the base of the leaf trace the arm to the right having the tracheids 'with a secondary look'.

The appendage to which Scott refers is a stout root and it is possible that its development in association with the base of the leaf trace may have been the cause of the local replacement of the primary tracheids by secondary ones though it should be pointed out that this is not generally the case.

The second example is one in the author's collection, and in this the stem has developed a well-defined cambium locally at one side of the primary xylem without however producing any recognizable secondary tracheids or phloem (Pl. **17**, fig. 8). The cause of this cambial development is quite obscure, and it rapidly dwindles in amount and disappears in the neighbouring sections of the series.

Whilst no apparent explanation can be found for such a case as this, secondary xylem which may be reasonably regarded as of traumatic origin, has been noted in a bifurcating stem in the Scott Collection and in a number of petioles. The Scott specimen, which occurs in slides numbered 2713 to 2720, is closely associated with a cortical wound fissure on either side of which the cells have subdivided to form a healing meristem several cells in depth. The series has already been described in some detail (Holden, 1930) and the section in which the secondary xylem is best developed has been figured both by Scott (1912, 1920) and the author. In this (slide no. 2715) and the one next above it in the series the added tissues, as seen in transverse section, form a more or less sickle-shaped strip lying on one flank of the stele. Where these tissues join the primary xylem they consist mainly of radially arranged parenchyma beyond which is a homogeneous layer of short, reticulately thickened tracheids (Pl. **17**, fig. 9).

Wounded petioles are not uncommon and trauma may on occasion result in the development of secondary xylem, though the production of a healing cortical meristem alone is more frequent. The most remarkable example of the production of traumatic secondary xylem so far discovered in a petiole is that figured in the present paper (Pl. **17**, fig. 10). In this petiole the xylem of the central bar is missing, and its place is occupied by a narrow fissure, on either side of which the parenchymatous cells have undergone division. Those on one side have produced several rows of radially arranged still parenchymatous daughter cells but those on the other have, in addition, produced a tangential plate of tracheids of small calibre from one to six cells in depth. In addition to these a mass of secondary tracheids appearing as a curved wedge in transverse section and also of smaller calibre than their primary counterparts, has been developed along the outside of one of the filaments, this wedge, in its widest part, being some ten cells in depth.

A further example of the production of a group of localized and asymmetrically situated secondary tracheids has also been found in two roots of *Diplolabis römeri*. I am indebted to the late Prof. W. T. Gordon for facilities for the examination of these specimens. The first shows a root in transverse section one pole of which is completely overarched by a C-shaped strip of small, more or less radially arranged tracheids six or seven cells in width in its widest part and thinning out to a single cell at its margins (Text-figs. 3–5). These tracheids are short and somewhat irregular in shape (Text-fig. 5) and show the reticulate thickening described as characteristic of the species by Gordon (1911*a*). Whilst proof of their development being due to wounding is lacking in this instance, their peculiar location and character strongly suggest that they are of traumatic origin. A similar interpretation seems probable in the case of the second root of this species also from the Gordon Collection. In this specimen, which is represented solely by its xylem, the metaxylem of the robust primary diarch plate is flanked on either side by a group of smaller, radially arranged tracheids more numerous on one side than the other (Pl. **17**, fig. 10). These smaller tracheids are not present in the neighbouring sections of the root, and it is unfortunate that the absence of phloem and cortex deprive us of what would be useful evidence.

The remaining palaeozoic ferns in which secondary thickening has been observed yield no clue as to the cause for its development. One of these, a specimen of *Metaclepsydropsis duplex* described by Gordon as a small axis (Gordon, 1911*b*), consists of a solid homogeneous core of primary tracheids completely enclosed by secondary xylem on the outer margins of which are evident traces of cambium (Pl. **17**, fig. 11). Unfortunately this axis lies near the edge of the section in which it occurs (slide no. 1233), and is absent from the adjacent slides of the series. The evidence for regarding it as a stem seems quite inadequate. There are no means of establishing its connexion with a neighbouring stem and it differs both in its structure and in its much smaller size from any of the recognizable stems in the Gordon material. It could with equal probability be interpreted as a stout root, and the fact that it shows the base of a lateral member which has all the appearance of a lateral root supports this interpretation. A second example, in this case an undoubted root, has been found in a specimen of *Austroclepsis* (*Clepsydropsis*) *australis*. This plant, which has been the subject of detailed study by the late Prof. Sahni (1928), was originally placed by him in the genus *Clepsydropsis*, but he transferred it to a new genus *Austroclepsis* in a subsequent paper (Sahni, 1932*b*). It had a *Tempskya*-like organization consisting of a number of relatively slender branching axes with their associated petioles all embedded in a dense sheath of adventitious roots.

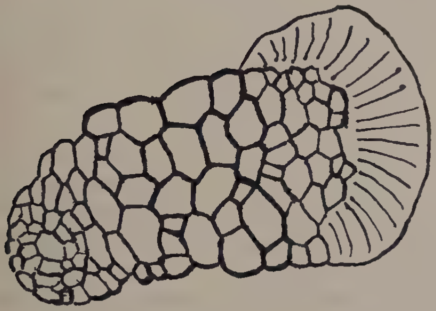

Fig. 3.

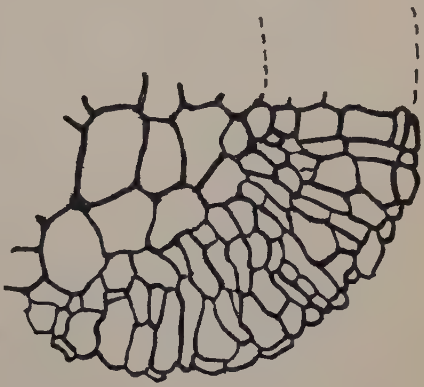

Fig. 4.

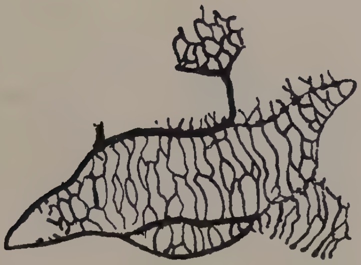

Fig. 5.

Text-figs. 3–5. Root of *Diplolabis römeri*. Fig. 3: transverse section of the stele showing the distribution of the secondary xylem; (×40); Fig. 4: a portion of the secondary xylem more highly magnified (×80); Fig. 5; a small group of the secondary tracheids to show their short irregular character and type of pitting (×400).

One of Sahni's specimens, that from Lyndon, New South Wales, contains an axis consisting of a solid mass of primary xylem almostly completely surrounded by a considerable thickness of secondary tracheids (Sahni, 1928; pl. V, figs. 50, 51). The continuity of the secondary xylem is broken on one side by a strip of parenchyma marking the region of emission of a small lateral trace. There is a close resemblance between the cortical tissues of this axis and those of normal roots, but Sahni does not commit himself to a firm opinion as to its nature. In the legend of his fig. 50 he refers to it as 'the enigmatical axis (stem or ? root)' and in the text (pp. 25, 26) under the heading *Axis of an unknown vascular plant* he suggests that it may be either a large root or that it 'belongs to some delicate plant which grew as an epiphyte on the false stem'. In a later paper, however (Sahni, 1932*b*), he describes it as a slender *Botrychioxylon*-like epiphytic among the roots of *Austroclepsis*. The fortunate discovery of an undoubted root of *A. australis* showing secondary thickening does much to resolve our doubts as to the nature of the axis in Sahni's specimen. This root, which is in the author's collection, shows an arc of secondary tracheids lying on either side of the primary metaxylem which is some five or six cells in depth at its widest point (Pl. **17**, fig. 13). These do not extend over and enclose the protoxylem poles. Opposite one of them, that to the right in fig. 13, there is an area of parenchyma extending to the endodermis which, in transverse section, has the shape of a partly open fan, but at the other pole the secondary tracheids have extended towards the mid-line leaving only a narrow strip of thin-walled cells opposite the protoxylem. These variations suggest that the primary xylem plate may be completely enclosed by secondary tracheids at a later stage and thus attain the condition shown in the section figured by Sahni.

In the two remaining palaeozoic ferns in which secondary thickening has been found it is confined to the stem. In neither case is it a constant feature nor is there any indication that it is traumatic in origin. One of these is the type specimen of *Grammatopteris rigolotti* originally described by Renault (1896), and more recently investigated in detail by Corsin (1937). The primary xylem of this stem which appears to have been more or less cylindrical is surrounded by a thin fringe of secondary xylem consisting of short, radially arranged tracheids possessing multiseriate pitting. A little of this secondary xylem accompanies the outgoing leaf trace at and near its point of origin but is soon lost. In this respect it shows a marked difference from the condition found in *Botrychioxylon* in which, as has been stated earlier, the major part of the xylem of the leaf trace at and near its base consists of secondary elements. It is an interesting fact that the co-type of *Grammatopteris rigolotti*, which has also been fully described by Corsin in the same paper, shows no trace of secondary xylem nor is there any indication of such tissue in *G. baldaufii* from the Lower Permian of Chemnitz (Sahni, 1932*c*).

The remaining palaeozoic fern stem in which what appears to be secondary xylem has been found is one of *Rachiopteris cylindrica* in the author's collection. This stem has been cut transversely at a point at which it is preparing to branch and has consequently assumed an oval outline. Closely associated with the stem at this level there are also four outgoing root traces. The stelar xylem of *R. cylindrica* normally consists of a central group of tracheids of small calibre surrounded by a homogeneous cylinder of larger tracheids (Bancroft, 1915). In this respect the stem under consideration is typical of the species, but it differs in possessing an outer, additional cylinder of smaller tracheids external to the larger ones (Pl. **17**, fig. 14). These peripheral smaller tracheids show few indications of radial arrangement, and their interpretation as secondary xylem is, on that account, possibly open to some doubt. It is a fact, however, that the cells of the conjunctive parenchyma immediately external to them have divided in a number of places to form flattened, cambiform daughter cells closely associated with adjacent immature tracheids. Whether this unusual development is a consequence of the association of branching and vigorous root formation can only be a matter for conjecture, though it does suggest a possible explanation of its occurrence.

We may summarize our present knowledge of the development of secondary xylem in palaeozoic ferns as follows:

1. Secondary thickening is a normal characteristic of both stem and root in *Botrychioxylon paradoxum* and *Zygopteris primaria*.
2. In *Ankyropteris corrugata* it is usually restricted to the larger roots but may be developed locally in the stem and at the base of the leaf trace. It may also be developed in both stem and petiole as a result of traumatic stimulus.
3. It is well developed in a root which has been provisionally assigned to an unknown zygopterid.
4. It may be developed as a traumatic response in the root of *Diplolabis römeri*.
5. Isolated examples of secondary thickening not attributable to wounding also occur in the stems of *Grammatopteris rigolotti* and *Rachiopteris cylindrica*, in a small axis, probably a root, of *Metaclepsydropsis duplex*, and in the root of *Austroclepsis* (*Clepsydropsis*) *australis*.

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EXPLANATION OF PLATES 16 AND 17

Plate 16

Fig. 1. Transverse section of the stele of a large root of *Ankyropteris corrugata* in which the secondary tracheids are replaced by parenchyma opposite the protoxylem groups. × 120.

Fig. 2. Transverse section of a root of *A. corrugata* showing the superficial origin of the periderm and one protoxylem pole completely arched over by secondary tracheids. × 60.

Fig. 3. Transverse section of the stele of a root of *A. corrugata* in which the secondary tracheids overarch both protoxylem poles. Immature flat tracheids are well shown on the lower side of the stele. × 80.

Fig. 4. Transverse section of young root of an unidentified fern in which the metaxylem plate is still incomplete: the papilliform surface cells are clearly shown on one side of the figure (Scott Coll. 3116). × 50.

Fig. 5. Transverse section of an old root of the same fern. Note the characteristic distribution of the secondary xylem, the immature secondary tracheids in the upper side of the xylem and the superficial periderm (U.C.L. Coll. J 25). × 36.

Fig. 6. Part of a longitudinal section of a similar root showing the divisions of the papilliform superficial cells to form part of the periderm (Scott Coll. 3115). × 36.

Fig. 7. Transverse section of part of a stem of *A. corrugata* showing an early stage in the emission of a leaf trace. Note the contrast between the xylem of the upper and lower poles (Williamson Coll. 245). × 40.

Plate 17

Fig. 8. Portion of the stele of a stem of *A. corrugata* showing localized cambium. × 40.

Fig. 9. Stele of a stem of *A. corrugata* showing an arc of secondary tissues (Scott Coll. 2715). × 25.

Fig. 10. Portion of a wounded petiole of *A. corrugata* showing secondary tracheids arching over one antenna and, at the bottom of the figure, similar tracheids replacing the central bar. × 40.

Fig. 11. Transverse sections. Solid axis (?root) of *Metaclepsydropsis duplex*. Traces of cambium are evident and the base of a lateral organ is shown at the bottom left-hand side of the figure. (Gordon Coll. 1233). × 50.

Fig. 12. Transverse section stele of a root of *Diplolabis römeri* showing the metaxylem of the primary plate with secondary tracheids on both sides. (Gordon Coll.). × 50.

Fig. 13. Transverse section of the stele of a root of *Austroclepsis* showing secondary thickening. × 30.

Fig. 14. Transverse section of the stele of a stem of *Rachiopteris cylindrica* showing small tracheids outside the ring of larger ones. Traces of cambium are shown on the left side. × 50.

H. S. HOLDEN

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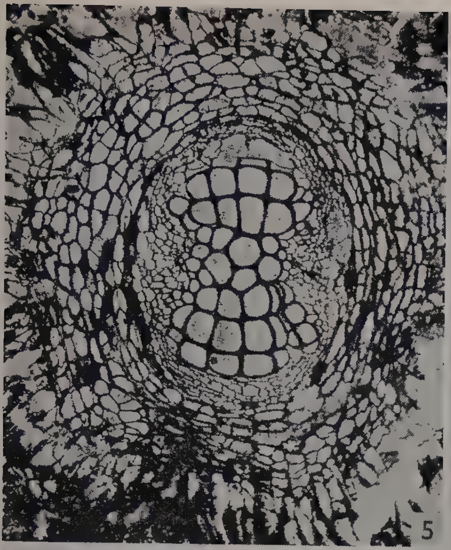
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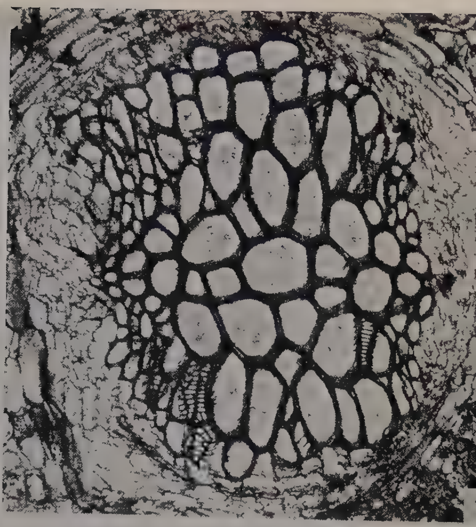

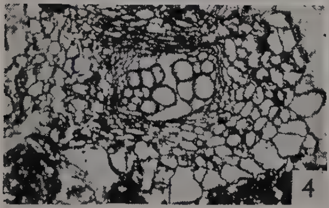
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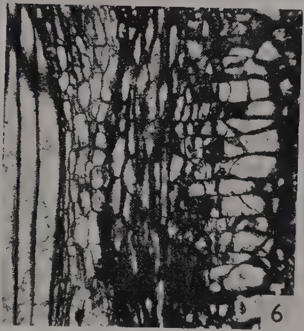
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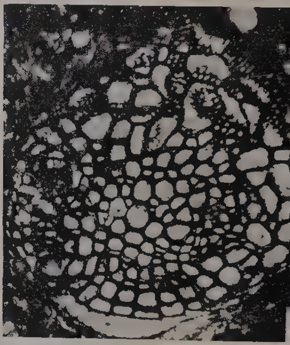

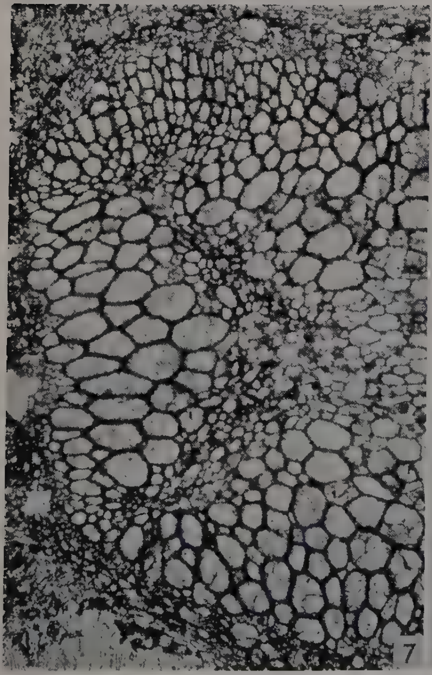
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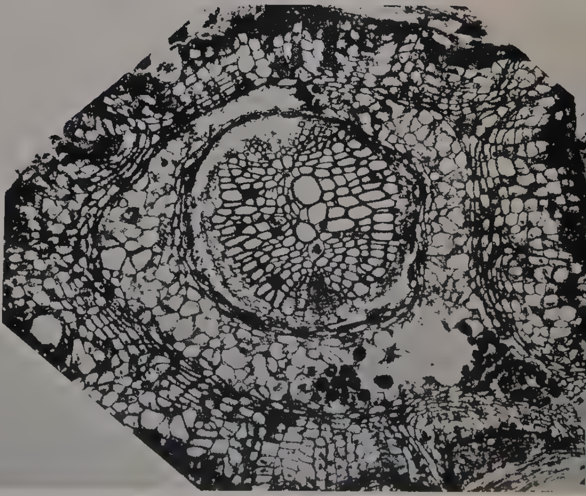
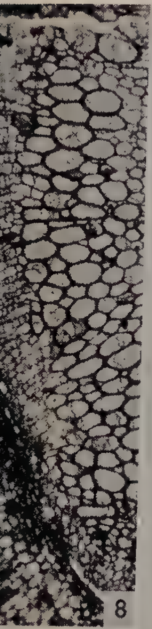


Sections of roots and stem of *Ankyropteris corrugata*, etc.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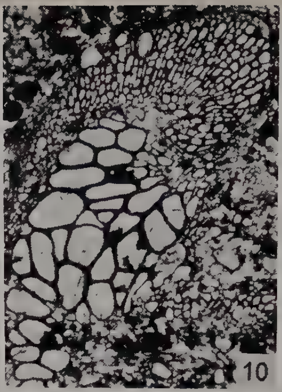
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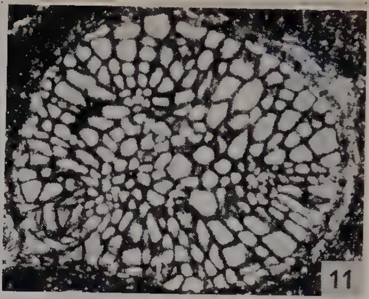
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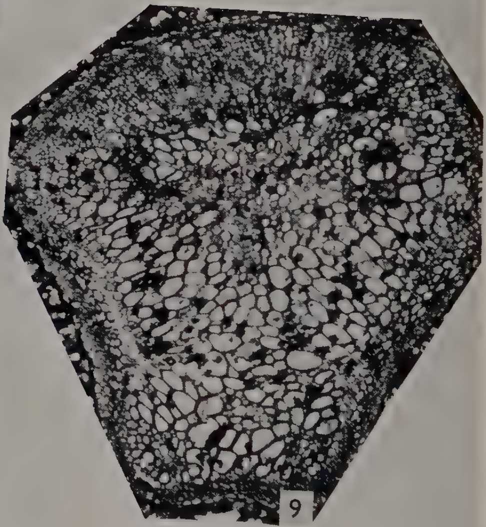
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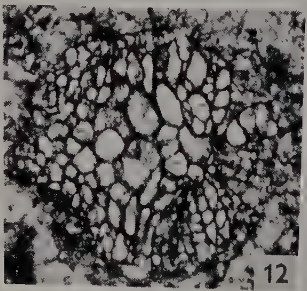
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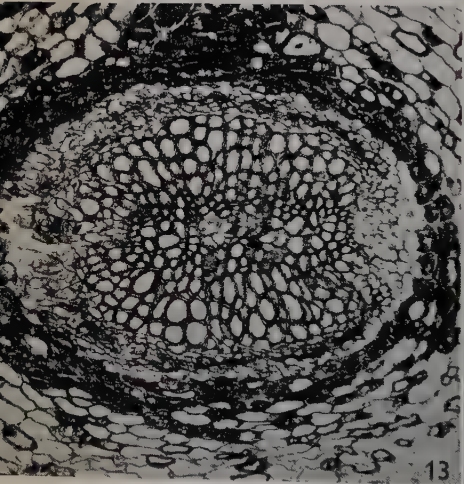
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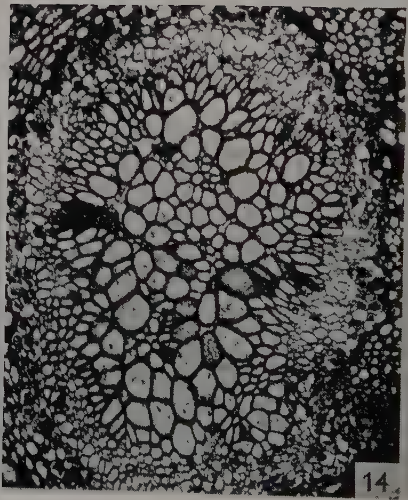
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Sections of various palaeozoic ferns

The morphology and growth of the vegetative and reproductive apices of Arabidopsis thaliana (L.) Heynh., Capsella bursa-pastoris (L.) Medic. and Anagallis arvensis L. By J. G. Vaughan, Chelsea Polytechnic.

(With Plates **18–21** and 4 Text-figures)

[Read 21 October 1954]

Introduction

In the past twenty years, an appreciable amount of research has been carried out into the growing points of angiosperms. This work, mainly anatomical and histological, has been facilitated by improved microtechnique. Most of the anatomical work published has concerned vegetative apices. Relatively few reproductive apices have been investigated, and there is even less anatomical information available on the transformation of the vegetative apex to the reproductive state. Several excellent reviews of the developmental anatomy of the shoot apex have appeared recently (Foster, 1939, 1941; Sifton, 1944; Majumdar, 1945; Philipson, 1949; Popham, 1951). The present paper deals with investigations that have been made into the apical morphology of *Arabidopsis*, *Capsella* and *Anagallis*. With the aid of a certain physiological technique, it has been possible to obtain material of two of these plants in all stages from the vegetative to the reproductive state. In describing the apices of the three plants under consideration, use has been made of the tunica-corpus and cyto-histological concepts, fully described in the reviews mentioned earlier in the introduction.

Material and methods

Both *Arabidopsis* and *Capsella* are rosette plants which frequently terminate in one main erect racemose inflorescence, but also other aerial flowering stems may arise in the axils of the rosette leaves. These aerial stems bear a small number of cauline leaves, in the axils of which arise subsidiary inflorescences. However, *Anagallis* is a procumbent herb which in the vegetative state branches profusely, although branches are not visible macroscopically until some distance behind the growing point. When the plant attains the flowering condition, flower buds develop in place of the vegetative buds. Apart from this, the general habit of the plant is the same as during the vegetative period.

Both *Anagallis* and *Arabidopsis* respond to photoperiodic treatment and are of the long-day type. *Anagallis* is an obligate long-day plant, that is, it will remain vegetative indefinitely if kept in light periods less than the critical of 12 hr. *Arabidopsis*, however, is described as a facultative long-day plant because it will flower eventually in short days (about 60) but, if plants in the vegetative state are exposed to continuous light or long-day periods, inflorescence buds soon appear.

For this investigation, *Arabidopsis* plants, 25 days old and which had been kept in short days, were exposed to continuous light for 8 days, at the end of which time inflorescence buds were quite obvious. During this period of illumination, samples of plants were fixed at day intervals and thus a complete transition from the vegetative to the reproductive state was obtained. A similar procedure was carried out in the case of *Anagallis*.

The *Capsella* plants were grown from seed in pots under normal conditions. Although not photoperiodically controlled, the various stages of development obtained for these plants could be interpreted from the controlled material of *Arabidopsis*.

The fixative employed during the investigation was formalin acetic-alcohol and serial sections were obtained in the usual manner. The *Arabidopsis* and *Capsella* material was stained with Heidenhain's haematoxylin alone but, in the case of the *Anagallis* material, aniline blue, according to the schedule of Popham, Johnson & Chan (1948), was employed as a counterstain.

THE VEGETATIVE AND REPRODUCTIVE APICES OF *ARABIDOPSIS* AND *CAPSELLA*

Inflorescence development

The general account of inflorescence development about to be presented deals specifically with *Arabidopsis*. No general account of inflorescence development in *Capsella* is presented because the process in both plants is essentially the same.

Text-fig. 1 A is a median longitudinal section of an *Arabidopsis* plant of the short-day type and therefore in the vegetative condition. The complete leafy axis is shown in the drawing. As one might expect from the rosette habit of the plant, the axis is very much condensed and the leaves and leaf primordia are attached to this axis very close to each other. No internodes are visible. The dense apex or promeristem can be seen in the centre of the drawing and, overlapping this, are the leaf primordia. The slightly convex shape of the apex is characteristic of *Arabidopsis* plants in the vegetative condition.

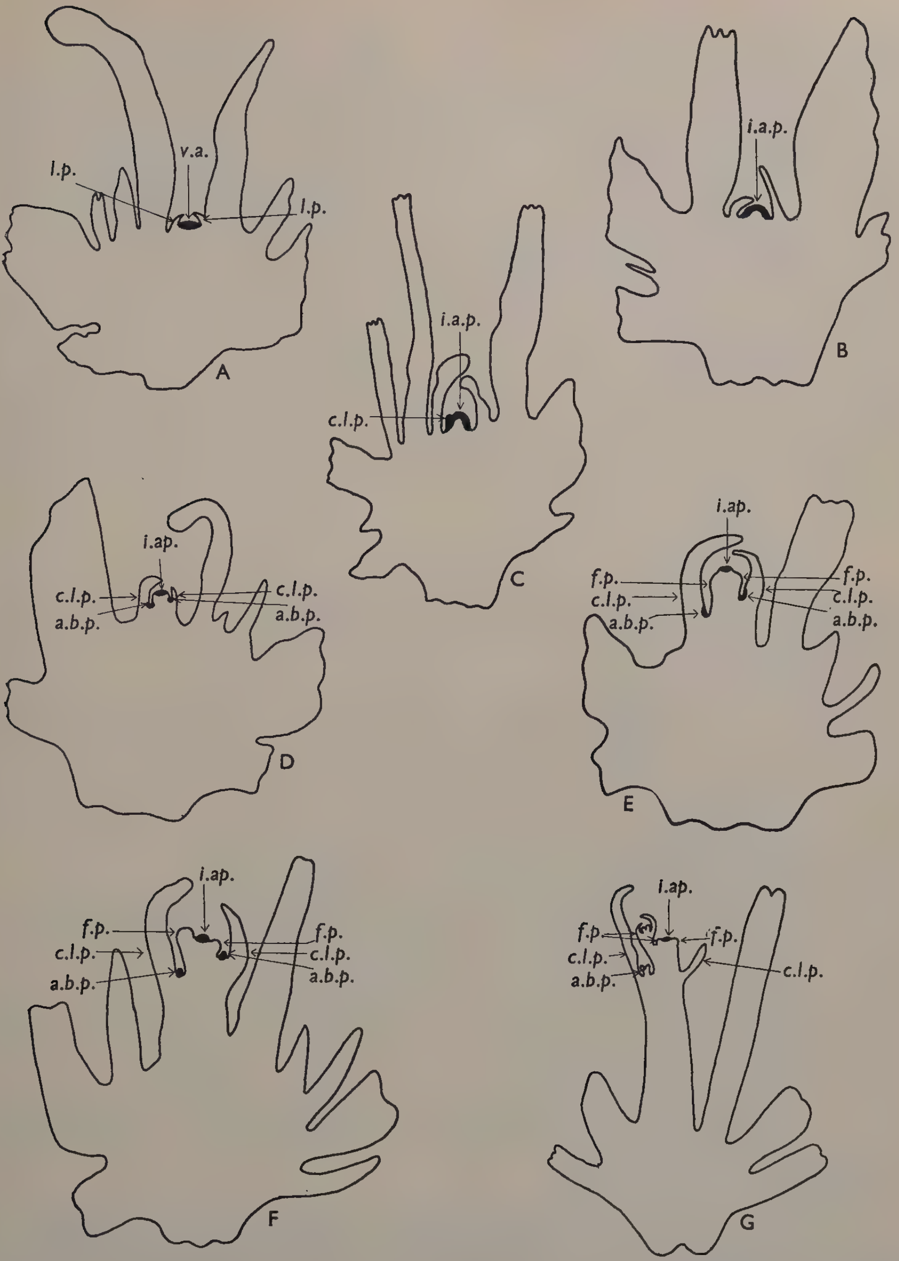
Under conditions of continuous light, in the first day, the plants remain in the vegetative condition and show the characters described in the previous paragraph.

In the second day of continuous light, however, changes are to be observed in a percentage of the sample examined. Text-fig. 1 B illustrates the condition shown by 75 % of the 2-day sample. It is the apex of the plant that has undergone a really important change. The shallow, slightly convex apex of the plant in the rosette condition has become a well-marked dome. Dense cells, as found in the rosette apex, occupy the apical region and flanks of this dome, but vacuolated cells are to be seen extending well up into its central region. The dome is the primordium of the inflorescence axis. If the series of sections from which Text-fig. 1 B was obtained is examined, cauline leaf primordia in the initiation stage will be found.

The plants fixed in 3 and 4 days of continuous light all show this inflorescence axis primordium in varying degrees of development. Text-fig. 1C is a longitudinal section of a third-day plant showing a more highly developed inflorescence axis, it having increased in height as compared with the one illustrated in Text-fig. 1 B. The apex is still dome shaped and shows the same general distribution of dense, meristematic tissue. The cauline leaf primordia have undergone further development, and Text-fig. 1 C shows such a primordium as a well-marked erection which does not overtop the main apex. This is in contrast to the state of affairs to be found in the rosette apex where leaf primordia, as soon as they are formed, overtop the main apex.

In the fifth day of continuous light, 50 % of the sample taken show just the initiation of the inflorescence axis, while the remaining 50 % show the first flower primordia. Text-fig. 1 D is of a 5-day plant of the type producing flower primordia. The dense inflorescence apex can be observed but no flower primordia are visible in this particular section. However, if the complete series of sections is examined, then two flower primordia can be observed. Two cauline leaves have been cut medianly and the older of the two, on the left-hand side of the axis, extends well above the apex; the younger, on the right-hand side of the axis, just curves over it. Small nests of dense cells are to be seen in the axils of these cauline leaves. These are the primordia of axillary buds which later give rise to subsidiary inflorescences.

In 6 days of continous light, 60 % of the sample taken show flower primordia, the rest just the primordium of the inflorescence axis in a very late stage of development. Text-fig. 1 E is a median longitudinal section of one of the 60 % of the 6-day sample which shows the typical condition. The main inflorescence apex and two flower primordia are shown in the figure. More flower primordia are to be found if the complete series of sections is



Text-fig. 1. (A) Longitudinal sections of an *Arabidopsis* plant of the short-day type (× 40). Two leaf primordia (*l.p.*) are shown growing over the slightly convex vegetative apex (*v.a.*) (B) Longitudinal section of an *Arabidopsis* plant exposed to 2 days of continuous light (× 40). Dense cells occupy the apex and the flanks of the inflorescence axis primordium (*i.a.p.*). (C) Longitudinal section of an *Arabidopsis* plant exposed to 3 days of continuous light (× 30). A cauline leaf primordium (*c.l.p.*) is shown which does not overtop the apex of the inflorescence axis primordium (*i.a.p.*). (D) Longitudinal section of an *Arabidopsis* plant exposed to 5 days of continuous light (× 30). Two cauline leaf primordia (*c.l.p.*) with their axillary bud primordia (*a.b.p.*) now overtop the inflorescence apex (*i.ap.*). (E) Longitudinal section of an *Arabidopsis* plant exposed to 6 days of continuous light (× 40). Two flower primordia (*f.p.*) are shown and the cauline leaf primordia (*c.l.p.*) with their axillary bud primordia (*a.b.p.*) have grown well above the inflorescence apex (*i.ap.*). (F) Longitudinal section of an *Arabidopsis* plant exposed to 8 days of continuous light (× 40). See (E) for explanation of labels. (G) Longitudinal section of an *Arabidopsis* plant exposed to 8 days of continuous light (× 19). See (E) for explanation of labels.

examined. Two well-developed cauline leaves with their axillary bud primordia curve over the apex.

Plants exposed to 7 and 8 days of continuous light all show flower primordia in varying degrees of development. Text-fig. 1 F is a median longitudinal section of an 8-day plant showing an advance in development over that illustrated in Text-fig. 1 E. The complete inflorescence axis has increased greatly in vertical extent. This is largely the result of longitudinal growth in that part of the axis below the insertion of the cauline leaves. The flower primordia are more advanced in development but are still enclosed by the cauline leaves. The axillary buds of these leaves are now very prominent.

Text-fig. 1 G is a median longitudinal section of another 8-day plant showing the furthest degree of development obtained with the plants examined. The main inflorescence axis has reached the height of about 2 mm. and, again, it is that part of the axis below the insertion of the cauline leaves that is responsible for this increase in length. The older flower primordia now show the initiation of all the flower parts. A change in connexion with the cauline leaves to be observed is that they are unfolding to expose the flower primordia. The axillary buds of these cauline leaves, at this stage, show the formation of lateral members.

Vegetative apex

The detailed structure of the vegetative apex of *Arabidopsis* is shown in Text-fig. 2 A and in Pl. **18**, fig. 1, which are of a median longitudinal section through the tip of a short-day plant.

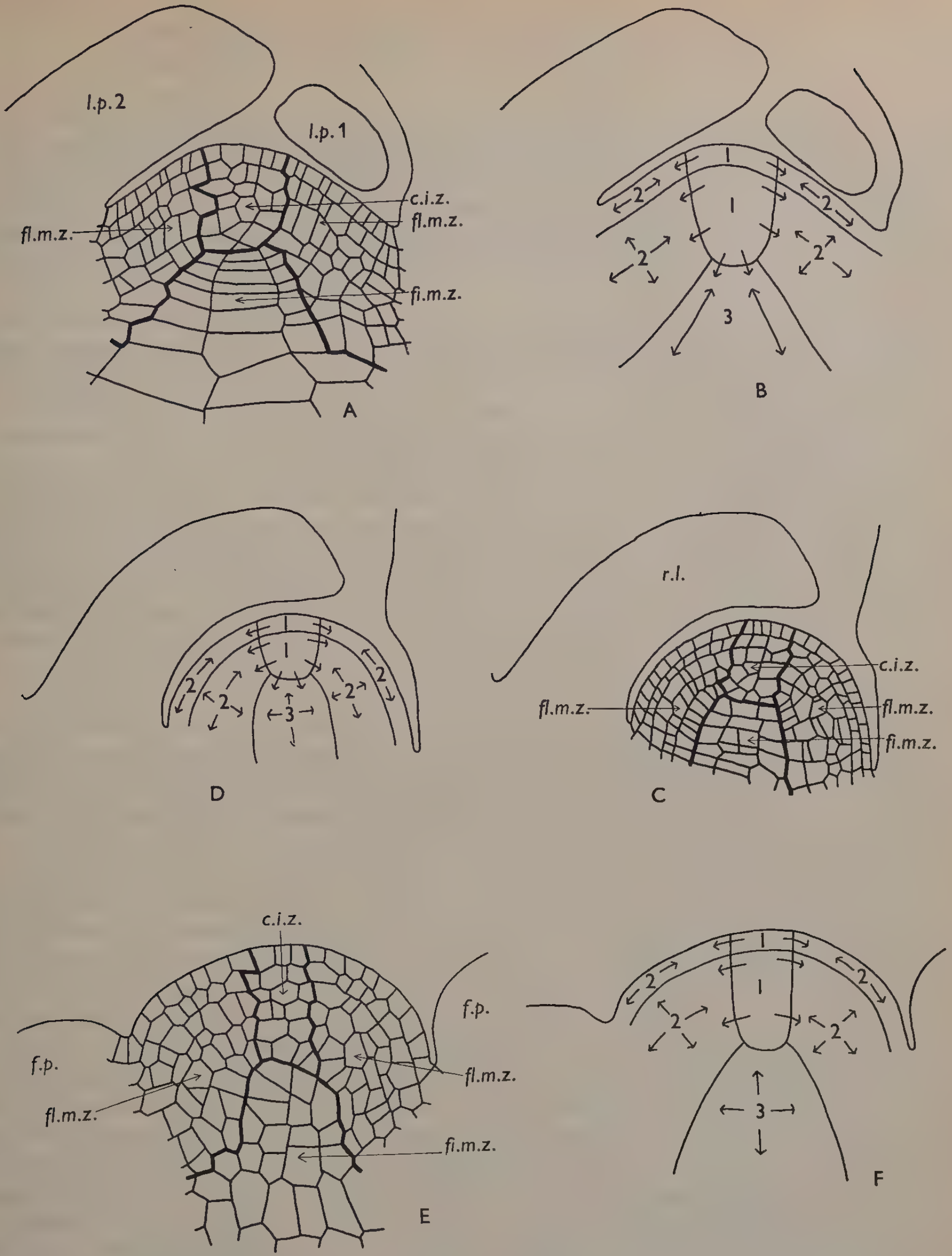
The youngest leaf primordium has not been cut medianly, but the next oldest primordium has been cut medianly and is shown curving over the left-hand part of the apex. As soon as rosette leaf primordia are formed, they overtop the main apex. The promeristem shown is cone-shaped, but a median longitudinal section through a recently initiated leaf primordium would present a slightly convex growing point. The width of the apex, at its widest part, is about 90μ and its height, in the centre, is about 35μ, and it is therefore one of the smallest apices to have been described.

In terms of the tunica-corpus concept, this promeristem has a tunica consisting of two layers of cells. Apices in all stages of the plastochrone have been examined, and the two surface layers show anticlinal divisions exclusively except when leaf primordia are initiated by periclinal divisions in the second tunica layer.

Also, zones can be recognized in the tunica and corpus of the apex which are characterized by cell size, density of contents and frequency of cell division. In the centre of this growing point, there is the central initiation zone which is bowl-shaped and consists of relatively few cells which show few divisions. Apart from those in the two surface tunica layers, the cells of this zone are arranged rather irregularly and, compared with the surrounding cells, they stain less deeply. The zone is about five cells deep in the middle and about three to four cells wide.

Surrounding the central initiation zone are the deeply staining cells of the flank meristem. Two sectors of this zone are shown in Text-fig. 2 A and in Pl. **18**, fig. 1. No obvious vacuolation is shown by the cells of the two zones already described and, in all cases, the nucleus occupies the major portion of the cell. No periclinal divisions are to be found, of course, in the two surface layers of the flank meristem and, although occasional periclinal divisions take place in the deeper layers, the zone as a whole presents a well-marked stratified appearance. It is about five or six layers of cells deep.

Below the central initiation zone is the third zone differentiated on cyto-histological grounds, the file or rib meristem. In Text-fig. 2 A and in Pl. **18**, fig. 1, this zone is represented by three vertical rows of cells, each consisting of about seven to nine units. The file meristem is perpetuated by the lowermost cells of the central initation zone and its cells show almost exclusively transverse divisions. The first file meristem cells to be produced, like most of the cells in the apical meristem, are very dense but, in contrast to



Text-fig. 2. (A) Longitudinal section of the *Arabidopsis* vegetative apex (× 725). The central initiation zone (*c.i.z.*), the flank meristem zone (*fl.m.z.*) and the file meristem zone (*fi.m.z.*) can be observed in the promeristem. The youngest leaf primordium (*l.p.* 1) and the next oldest primordium (*l.p.* 2) can also be seen. (B) Diagrammatic longitudinal section of the *Arabidopsis* vegetative apex to show the positions of the main growth zones and the direction of cell divisions. 1, the central initiation zone; 2, the flank meristem zone; 3, the file meristem zone. The tunica runs through the central initiation and the flank meristem zones. (C) Longitudinal section of the *Arabidopsis* inflorescence primordium (× 359). The central initiation zone (*c.i.z.*), the flank meristem zone (*fl.m.z.*) and the file meristem zone (*fi.m.z.*) can be observed in the promeristem. A rosette leaf (*r.l.*) is to be seen growing over the apex. (D) Diagrammatic longitudinal section of the *Arabidopsis* inflorescence primordium to show the position of the main growth zones and the direction of cell divisions. 1, the central initiation zone; 2, the flank meristem zone; 3, the file meristem zone. The tunica runs through the central initiation and the flank meristem zones. (E) Longitudinal section of the *Arabidopsis* inflorescence apex (× 438). The central initiation zone (*c.i.z.*), the flank meristem zone (*fl.m.z.*) and the file meristem zone (*fi.m.z.*) can be observed in the promeristem. Parts of two flower primordia (*f.p.*) are also shown. (F) Diagrammatic longitudinal section of the *Arabidopsis* inflorescence apex to show the positions of the main growth zones and the direction of cell divisions. 1, the central initiation zone; 2, the flank meristem zone; 3, the file meristem zone. The tunica runs through the central initiation and the flank meristem zones.

the cells which give rise to them, they are very much flattened. About the first three cells of each file meristem row are of this appearance and then vacuolation promotes cell extension, mainly in the lateral direction. Little vertical extension occurs. The collection of the first few dense flattened cells of the file meristem has been referred to as a 'cambium-like' zone. A characteristic feature of the *Arabidopsis* rosette axis is that the regular file meristem cells give rise almost immediately to the disorganized, highly vacuolate cells of the pith.

Tiny bud primordia have been observed in the axils of the mature rosette leaves and, occasionally, they undergo further development but it was not possible to trace their development in detail.

In the case of *Capsella*, rosettes, measuring about half an inch across, provided apices in the vegetative condition. Essentially, the structure of the *Capsella* apex is the same as that of *Arabidopsis*.

The cyto-histological zones, to be observed in longitudinal sections of the *Arabidopsis* vegetative promeristem, can also be seen in transverse sections (Pl. **18**, figs. 2, 3). The plant being of the rosette habit, numerous leaves and leaf primordia with prominent median vascular strands are shown in the photographs. Some of the primorida show marginal meristems. In Pl. **18**, fig. 3, at one point, the flank meristem is expanded laterally. This is the foliar foundation on which the next leaf primordium will be erected. In this photograph, both the youngest and the next youngest leaf primordia show well-marked abaxial vacuolation.

Significant roles can be attached to all the zones found in the vegetative apices of *Arabidopsis* and *Capsella*. The surface tunica gives rise to the epidermal system of the plant. The flank meristem is concerned with the production of leaf primordia, their associated procambial strands and the cortex; the file meristem gives rise to the pith and the central initiation zone is a self-perpetuating region of the apex producing new flank and file meristem (Text-fig. 2*b*).

The growth of the *Arabidopsis* apex has been studied in some detail. In Text-fig. 2A and Pl. **18**, fig. 1, two sectors of flank meristem are shown both presenting the stratified appearance characteristic of the zone. When sufficient flank meristem has been reconstituted by the central initiation zone to form a foliar foundation, leaf initiation takes place in that sector. This process is brought about by periclinal divisions in the second tunica layer. At the erection of the leaf primordium, the stratified appearance of the foliar foundation is lost and a considerable amount of cell reorganization takes place. Probably, the most important feature of this re-organization is the establishment of the procambial supply which runs into the developing primordium. Vacuolation then takes place in the foliar foundation and its leaf primordium, starting first in the abaxial side of the foliar foundation and extending up into the abaxial side of the primordium and then proceeding similarly on the adaxial side (Pl. **18**, fig. 1). During this vacuolation, the procambium becomes very evident. At all times, the leaf procambium develops acropetally from the existing network. Apical and marginal meristems can be recognized in the further development of the leaf primordium. The foliar foundation having undergone vacuolation, more flank meristem is reconstituted by the central initiation zone to take its place. These flank meristem cells, as they are produced, themselves undergo repeated anticlinal divisions to increase the area of the zone. The relatively few periclinal divisions that occur increase the depth of the flank meristem. The avidity for stain shown by the cells of this zone, in contrast to the central initiation cells, may be ascribed to the greater amount of division that takes place in the flank meristem.

The file meristem produces the pith, and *Arabidopsis* is peculiar in that there is a sharp transition between the regular vertical rows of the file meristem and the highly vacuolate, disorganized cells of the pith. There is not such a marked transition in *Capsella*. Text-fig. 2A and Pl. **18**, fig. 1, show the file meristem of *Arabidopsis* at its greatest development. This type of development seems to be associated with the mid-phase of the plastochrone, and this is to be expected because the real importance of the zone is to produce pith cells to accompany the developing leaf and leaf base. As will be mentioned later, good development of file meristem brings about a well-marked increase in the length of the axis and the poor development of file meristem and its sudden transition to pith in *Arabidopsis* and *Capsella* is to be associated with the rosette habit of the plant for, here, internodes are absent and pith is only formed in conjunction with a relatively small area of leaf base.

The following account of the development of the inflorescence of *Arabidopsis* shows how the completely vegetative apex is directly converted into the apex of the inflorescence primordium.

Text-fig. 2C and Pl. **18**, fig. 4, show the apex of the *Arabidopsis* plant illustrated in Text-fig. 1B at a higher magnification, at an early stage of the transition from the vegetative to the reproductive phase. In contrast to the fairly shallow, slightly convex rosette apex, the apex now under consideration is quite a large dome-shaped structure. The dense, meristematic cells, characteristic of any active growing point, extend well down the flanks of this apex and its height is about 75μ and its width, at the base, is about 90μ. Pl. **18**, fig. 5, shows a later stage of inflorescence formation in *Capsella*. The rosette from which this preparation was made measured about three-quarters of an inch across.

Although a well-marked change has taken place in the shape and form of the apex, the two-layered tunica and the cyto-histological zones can still be recognized but, however, the file meristem has undergone quite a remarkable development. Compared with the truly vegetative apex, many more transverse and longitudinal cell divisions have taken place in the zone while the cells have elongated considerably in the longitudinal direction. These differences are particularly noticeable in Pl. **18**, fig. 5, and they are responsible for the initiation of the flower-bearing axis.

At this stage of development, cauline leaf primordia are initiated. Pl. **18**, fig. 6, has been taken from the same series of sections as Pl. **18**, fig. 4, and Text-fig. 2C, and shows the initiation of such a primordium by periclinal divisions in the second tunica layer. At this stage, at least, the primordium does not curve over the main promeristem and the development of its procambium supply, like that of the rosette leaf primordia, is acropetal.

A quite characteristic feature of the type of apex under discussion is the retention of fairly large areas of flank meristem which enclose the vacuolating and dividing file meristem (Text-fig. 2D). It would seem that the maturation of this flank meristem lags behind that of the file meristem, and this is borne out by the fact that cauline leaf primordia, produced in the flank meristem, do not overtop the main promeristem for some time. This is in contrast to the state of affairs in the rosette apex.

As has been explained in an earlier paragraph, the apex just described soon produces flower primordia and Pl. **19**, fig. 1, and Text-fig. 2E, are median longitudinal sections of a typical *Arabidopsis* inflorescence apex. The plant from which it was taken was exposed to 7 days of continuous light and was actively producing flower primordia. Two of these primordia, cut obliquely, are shown in the illustrations.

The dome-shaped apex is about 75μ across at its widest part and about 45μ deep in the centre. It possesses a two-layered tunica which is not disturbed at all during its growth processes, even at the initiation of a flower primordium. An examination of numerous series of sections has confirmed this observation. There is no great distinction between the central initiation and flank meristem zones on staining qualities, but investigations of the apex throughout its growth cycle have revealed the presence of a self-perpetuating zone. The flank meristem zone is five or six layers of cells deep.

Vacuolating file meristem is to be seen developing from the lowermost part of the central initiation zone. The first cells produced are rectangular with their long axes at right angles to the main longitudinal axis of the plant, but soon cell extension takes place and the condition is reversed. Transverse divisions, of course, predominate here, but also a number of longitudinal divisions occur to widen the zone.

As in the rosette apex, important roles can be ascribed to the zones of the inflorescence growing point. The flank meristem is concerned with the production of the lateral members, the flowers, their associated procambium and the cortex, while the actively dividing file meristem produces the pith of the inflorescence axis. Reconstitution of these zones is carried out by the central initiation zone (Text-fig. 2F).

Pl. **19**, fig. 2, and Text-fig. 3A, are median longitudinal sections of an *Arabidopsis* inflorescence apex showing the initiation of a flower primoridium in the right-hand sector of the flank meristem. Periclinal divisions in the third layer of this zone are primarily responsible for the flower primordium initiation, and the cells of this layer in the illustrations are either actively involved in this type of division or are elongating prior to it. The cells of the two tunica layers overlying the point of initiation present a very compressed appearance and seem recently to have undergone repeated anticlinal divisions. Divisions in various planes have taken place in the fourth and fifth layers of the sector of flank meristem under consideration.

The sector being described extends for some distance down the longitudinal axis of the inflorescence and here the flank meristem can be regarded as having reached its full development. In longitudinal section, about ten cells of the third flank meristem layer are involved in this initiation. As will be described later, the flank meristem involved in this flower primordium production soon undergoes vacuolation and maturation and the central initiation zone, to be seen in Pl. **19**, fig. 2, produces more of the zone from part of its flanks. Pl. **19**, fig. 1, and Text-fig. 2E, F, show the reconstitution of flank meristem on either side of the central initiation zone. Active anticlinal and some periclinal divisions are responsible for the rapid growth of this important peripheral zone.

The apex of the *Capsella* flowering axis agrees in all respects with that of *Arabidopsis*.

Comparison of inflorescence and vegetative apices

A comparative study of the rosette and inflorescence growing points of the two members of the Cruciferae under consideration brings to light some important morphological similarities and differences.

Although these apices themselves vary in shape during their growth processes, an overall difference between the two types can be observed. The vegetative apex is never more than slightly convex while the inflorescence apex is always markedly dome-shaped. A reason for this difference will be suggested later.

As far as can be observed, the tunica of the rosette apex is always biseriate, only being disturbed at leaf initiation. A two-layered tunica is also characteristic of the inflorescence apex and is retained even at flower primordium initiation.

Central initiation, flank meristem and file meristem zones are to be found in both types of growing point and they perform the same general functions, but the flank and file meristem zones vary as regards extent of development and activity in the two different apices. It has been shown that quite an appreciable longitudinal sector of flank meristem needs to be reconstituted by the central initiation zone before flower primordium formation can take place. A smaller sector is needed in the rosette apex for the establishment of a foliar foundation and the resulting leaf primordium.

In the rosette apex the file meristem is of very limited development, quickly giving rise to the disorganized pith. On the other hand, the file meristem in the inflorescence apex shows a very extensive development, exhibiting numerous active transverse and longitudinal divisions. Cell extension is also marked in this file meristem, the cells elongating in a plane parallel to the longitudinal axis of the inflorescence. It would seem that, in any growing axis, it is the activity of the file meristem zone of the apex of that axis that determines the extent of its vertical growth and, therefore, in the vegetative apices of the rosette plants under discussion, the poor development of file meristem foreshadows the condensed nature of the axis. On the other hand, very active growth of the file meristem gives a clear indication that the elongating axis will become an inflorescence.

The shapes of the two different types of growing point, so far described, can be correlated with their characteristic growth processes. In the rosette apex, the file meristem zone promotes little vertical extension, so that a comparatively small sector of flank meristem is required to form a foliar foundation, and consequently the shape of the apex is slightly convex. In the inflorescence apex, however, the file meristem is promoting very active vertical extension and a comparatively large sector of flank meristem is required for flower primordium formation. While this flank meristem is being reconstituted, the activity of the file meristem produces a markedly domed apex.

Flower primordium

The third type of shoot apex in *Arabidopsis* and *Capsella* is, of course, that of the flower, and it is of interest to investigate the development and activity of this growing point.

It has been shown (Pl. **19**, fig. 2 and Text-fig. 3 A) that a flower primordium is initiated by periclinal divisions mainly in the third flank meristem layer of the inflorescence promeristem. Numerous mitotic divisions then take place in the protuberance thus produced, and raise the level of its apex above that of the main inflorescence axis. At this stage, the primordium consists almost entirely of dense, meristematic cells, but vacuolation soon occurs to delimit the future pedicel and receptacle. A *Capsella* flower primordium, in such a condition, is shown in Pl. **19**, fig. 3. Considerable vacuolation has taken place in the peripheral areas of the future pedicel region with the result that the procambium is well marked. The future flower receptacle consists of typical, meristematic cells and shows the biseriate tunica, characteristic of both the vegetative and inflorescence apices. A corpus, too, is present consisting of a few layers of irregularly dividing cells. In Pl. **19**, fig. 3, the initiation of the first pair of sepals, by periclinal divisions in the second tunica layer, can easily be seen. The developing sepals soon show vacuolation in their abaxial halves which causes them to curve over the flower apex. Further growth is promoted by apical and marginal meristems. The initiation and development of the second pair of sepals are, in all respects, similar to those of the first pair.

Stamen initiation in *Capsella* is shown in Pl. **19**, fig. 4, which is of a longitudinal section of a flower primordium taken through the median plane of the second pair of sepals. Compared with Pl. **19**, fig. 3, there have obviously been a number of cell divisions in the corpus zone, and also the cells have become vacuolated. Most of the remaining dense meristematic cells form the biseriate tunica, in the second layer of which the stamen primordia have been initiated by periclinal divisions.

Following stamen initiation, the remainder of the flower primordium apex is given over to the formation of the terminal gynaeceum. Pl. **19**, fig. 5, shows how this last essential organ has been initiated by numerous periclinal divisions in the second tunica layer.

In the preceding account of flower part development, no mention has been made of petal initiation and development. Rather curiously, petal primordia are not easily seen in the young flower buds of *Arabidopsis* and *Capsella*. Pl. **19**, fig. 6, is of a longitudinal section of an *Arabidopsis* flower bud with quite well-developed sepals, stamens and gynaeceum. In the right half of the photograph, just inside the base of one of the sepals, is to be seen a small mound of dense, meristematic tissue with a single tunica layer. This is a petal primordium, and above it is a dense stamen anther. The retarded development of the petals is strange when one considers the comparatively large size which they finally attain. Although a study of petal initiation and development offers a number of practical difficulties in *Arabidopsis* and *Capsella*, it is thought that actual initiation follows that of the second pair of sepals.

A study has been made of the development of procambium in the flower primordia and floral parts of the two members of the Cruciferae under consideration and the provascular meristem has always been found to develop in a continuously acropetal manner from the existing system. Pl. **19**, fig. 7, shows the acropetal development of procambium to two young *Capsella* flower primordia from the system already present in the inflorescence axis. The further acropetal development of procambium to the *Capsella* flower parts is shown in Text-fig. 3 B–D. The provascular meristem of the flower receptacle which grows into the developing stamens and gynaeceum differs from normal procambium in that its cells are merely brick-shaped, not elongated, and also in that the contents of its cells are not particularly dense. These differences make the identification of this type of procambium rather difficult, but it has always been found to develop continuously from the existing system. No definite statement can be presented regarding the mode of provascular meristem development to the petals because of their late maturation.

THE VEGETATIVE AND REPRODUCTIVE APICES OF *ANAGALLIS*

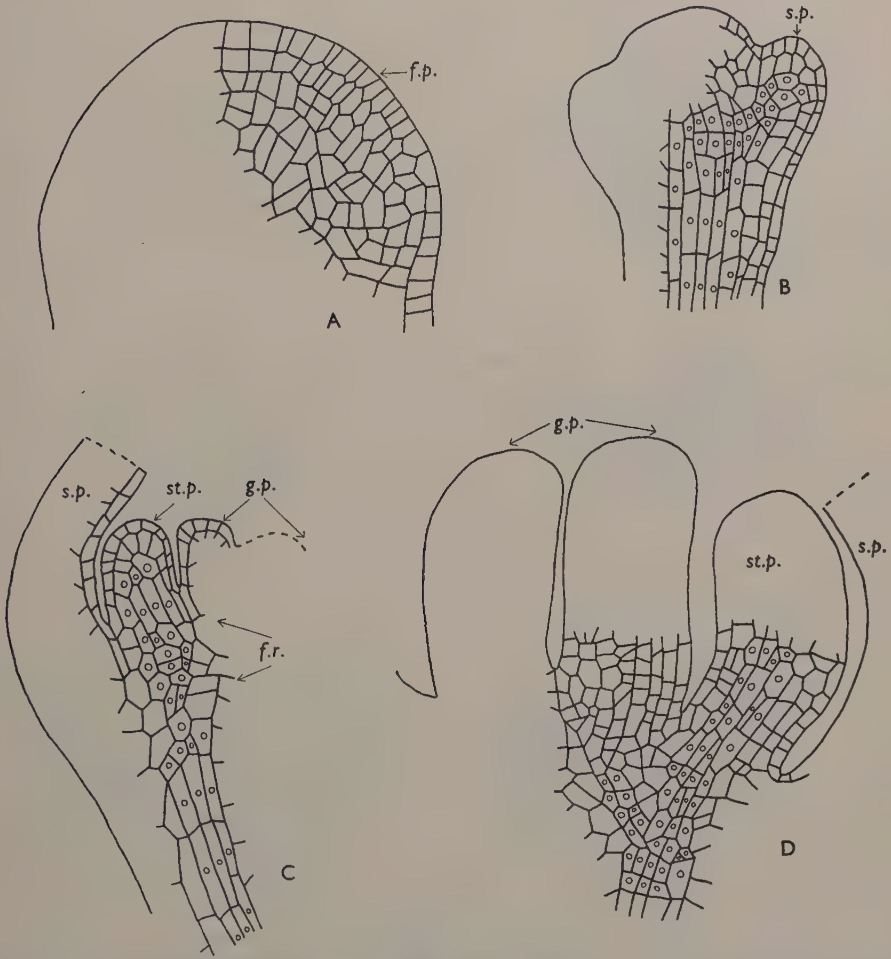
All the growth zones, described for the vegetative apices of *Arabidopsis* and *Capsella*, are to be found in the corresponding apex of *Anagallis* and this plant, with its regular opposite and decussate phyllotaxis, is ideal for tracing the development of the zones throughout the course of a plastochrone.

Vegetative apex

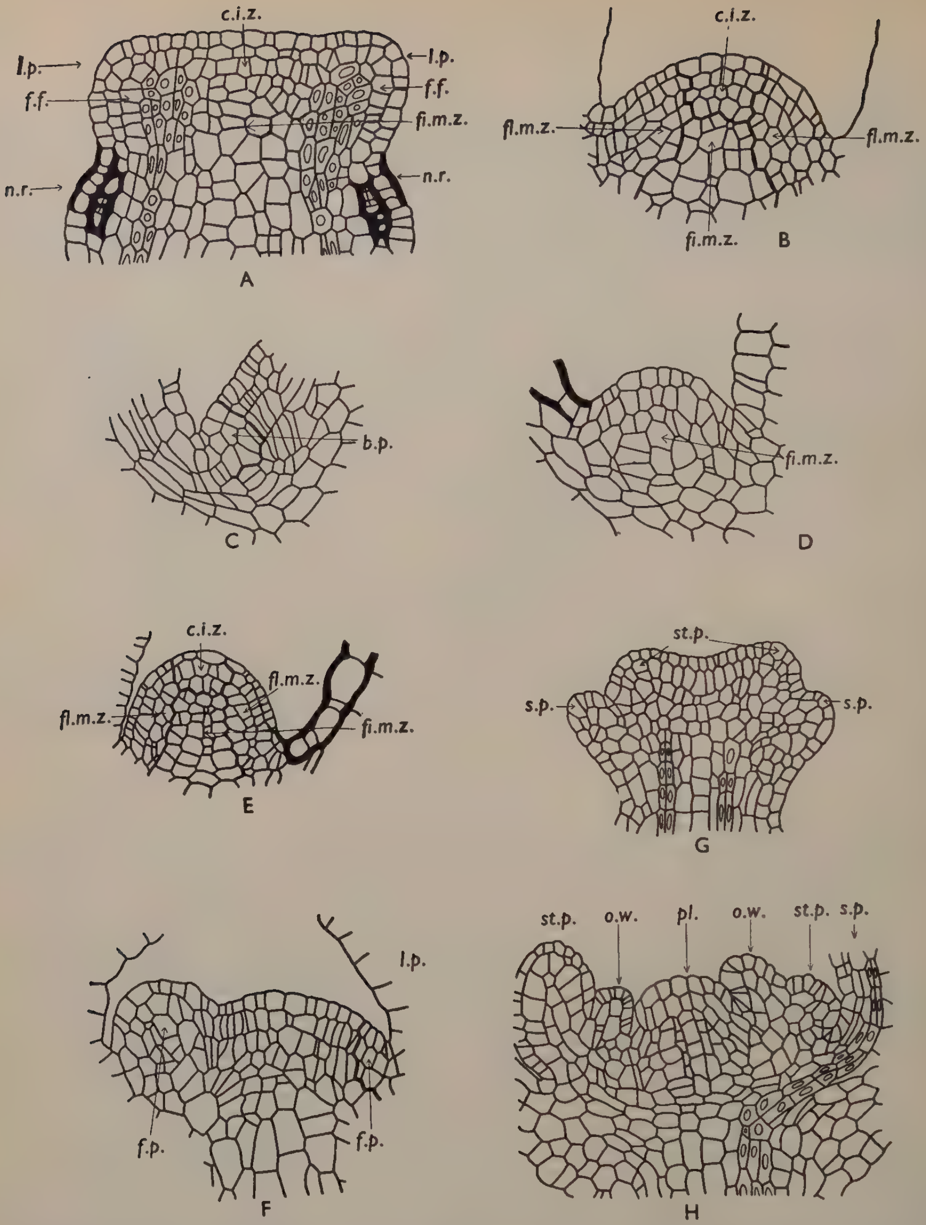
Pl. **20**, fig. 1, and Text-fig. 4 A, are of a median longitudinal section through the *Anagallis* vegetative apex showing the initiation of a pair of leaf primordia. The two opposite primordia are represented as small elevations, and they are still based on dense meristematic tissue, the foliar foundations. The actual apex, in between them, has been reduced to its minimal area and is quite flat. Its width, between the two primordia, is about 60 μ. Below the apex and its foliar primordia can be seen a swollen, vacuolated region. This is the nodal region of the last pair of leaf primordia to have been formed. These primordia are arranged at right angles to the ones shown in the illustrations. The nodes of this plant are characteristic in that the cell walls of the two surface layers of cells undergo considerable thickening which, in addition to well-marked periclinal divisions in the second layer, produce the swollen appearance.

The foliar foundations, mentioned earlier, do not present a stratified appearance and it is obvious that, in these regions, a number of cell divisions and some reorganization have taken place. The leaf primordia themselves appear to have been raised by periclinal divisions in the second layer from the surface. An outstanding feature of reorganization in the foliar foundations is the establishment of procambium which can be seen running through the dense cells of the apical meristem, in both leaf primordia, to within three cells of the apices of the primordia. The procambium, in the foliar foundations, can be seen to be continuous with the procambium of the swollen node and internode previously mentioned so that the development of procambium to the leaves of this plant is regarded as acropetal.

Considering that part of the apex within the foliar foundations, a well-marked stratification can be observed. The two surface layers show no periclinal divisions, and so the vegetative apex of this plant is regarded as having a biseriate tunica. However, the remaining dense meristematic cells of that part of the apex now under consideration show various periclinal and oblique divisions and some of the products of these divisions give rise to vacuolated cells which must be regarded as constituting the file meristem. The vacuolation of these cells causes them to elongate in a plane parallel to the longitudinal axis of the plant. Transverse divisions predominate in this zone, but longitudinal divisions are also to be observed, which serve to increase the diameter of the axis. The central cells of the surface layer of the apex between the two foliar foundations are much larger than the remaining cells of this layer. Anticlinal divisions are very prominent in the smaller cells of the surface layer. The central initiation cells of the apex under consideration are regarded as those including and below the very large central cells of



Text-fig. 3. (A) Longitudinal section of the *Arabidopsis* inflorescence apex showing the initiation of a flower primordium (*f.p.*) by periclinal divisions in the third flank meristem layer from the surface (× 666). (B) Longitudinal section of part of a *Capsella* flower primordium (× 339) taken through the median plane of the first pair of sepal primordia (*s.p.*). The cells with the nuclei drawn in form the procambium and it can be seen that this tissue is developing acropetally from the pedicel provascular meristem into the right hand sepal primordium. (C) Longitudinal section of part of a *Capsella* flower primordium (× 301) showing a sepal primordium (*s.p.*), a stamen primordium (*st.p.*) and the gynaeceum primordium (*g.p.*). The cells with the nuclei drawn in form the procambium and the continuously acropetal development of this tissue to the stamen primordium (*st.p.*) from the pedicel is shown. The procambium cells in the flower receptacle (*f.r.*) are rather brick-shaped. This is in contrast to the normal state of affairs where the provascular meristem cells are very much elongated. (D) Longitudinal section of part of a *Capsella* flower primordium (× 444) showing the gynaeceum primordium (*g.p.*), a stamen primordium (*st.p.*) and part of a sepal primordium (*s.p.*). The cells with the nuclei drawn in form the procambium and the continuously acropetal development of this tissue to the gynaeceum primordium (*g.p.*) is shown.



Text-fig. 4. (A) Longitudinal section of the *Anagallis* vegetative apex (× 251) at minimal area showing two leaf primordia (*l.p.*), the central initiation zone (*c.i.z.*), the file meristem zone (*fi.m.z.*), the foliar foundations (*f.f.*) and the swollen nodal region (*n.r.*). The cells with the nuclei drawn in form the procambium. (B) Longitudinal section of the *Anagallis* vegetative apex (× 245) at maximal area. For explanation of labels see fig. A; in addition, the flank meristem zone (*fl.m.z.*) is shown. (C) Median longitudinal section (× 250) showing an *Anagallis* bud primordium (*b.p.*) in the axil of one of the second pair of leaves of the main vegetative axis. (D) Longitudinal section (× 275) showing an *Anagallis* bud primordium in the axil of one of the fourth pair of leaves of the main vegetative axis. The file meristem zone (*fi.m.z.*) is now quite well developed. (E) Longitudinal section of an *Anagallis* axillary vegetative bud (× 200) showing the central initiation zone (*c.i.z.*), the flank meristem zone (*fl.m.z.*) and the file meristem zone (*fi.m.z.*). (F) Longitudinal section of the *Anagallis* inflorescence apex (× 275) taken through the median plane of the first pair of leaf primordia (*l.p.*). Two axillary flower primordia (*f.p.*) are shown. (G) Longitudinal section of an *Anagallis* flower primordium (× 200) showing sepal primordia (*s.p.*) and stamen primordia (*st.p.*). The cells with the nuclei drawn in form the procambium. (H) Longitudinal section of an *Anagallis* flower primordium (× 208) showing a portion of a sepal primordium (*s.p.*), portions of two stamen primordia (*st.p.*), the developing ovary wall (*o.w.*) and the developing placenta (*pl.*). The cells with the nuclei drawn in form the procambium.

the surface layer. Pl. **20**, fig. 2, and Text-fig. 11 B, show the apex at or just before leaf initiation. The new pair of leaf primordia will be formed in the flank meristem at right angles to those shown in the illustrations. During the course of the plastochrone, the apex increases in size until, at this stage, it measures about $120\,\mu$ across at its widest part and presents a marked convex appearance which contrasts strongly with its flat appearance at minimal area.

The two-layered tunica is very obvious, and the cyto-histological zonation is seen at its best. The central initiation cells of the surface tunica layers, by reason of their large size and vacuolated contents, contrast strongly with the rest of the cells of the layer. A regular appearance is presented by the central initiation zone except at its basal region where various oblique divisions are taking place to give rise to the file meristem. This vacuolated zone is now well encircled by flank meristem and shows its usual regular cell divisions. The dense flank meristem has grown to its full extent and appears to have reached its maximum depth of five layers of cells. As the apex enlarges during the period of the plastochrone, anticlinal divisions are mainly responsible for the growth of the flank meristem and, also, periclinal and oblique divisions serve to increase the depth of the zone and these divisions seem to take place mainly in the third layer of flank meristem.

As has been explained earlier, vegetative lateral buds are not visible macroscopically in *Anagallis* until the third or fourth node from the apex. However, some interesting information concerning their development is forthcoming if sections of the youngest nodes are prepared and examined microscopically.

Pl. **20**, fig. 3, and Text-fig. 4 C, are of a longitudinal section taken medianly through the second pair of the leaf primordia and, in the axil of one of them, is the first indication of axillary bud formation. The bud primordium is represented as a small nest of dense, meristematic cells. An interesting feature of its formation is that it has obviously been isolated from the main apical meristem by vacuolating cells which are very much compressed. There is no question of previously vacuolated cells regaining their meristematic properties to form this primordium. The bud primordium possesses a biseriate tunica developed from the tunica of the main promeristem. The rest of the primordium consists of a single layer of cells which are elongating at right angles to the apex surface prior to periclinal divisions.

In Pl. **20**, fig. 4, and Text-fig. 4 D, a bud primordium, in the axil of one of the fourth pair of leaves, is to be seen bulging above the plant surface. The biseriate tunica is intact and the increase in height of the primordium can be attributed to the production of dividing file meristem by the third layer of dense, meristematic cells mentioned in the previous paragraph. There are indications, too, of the establishment of a flank meristem zone. An older bud, shown in Pl. **20**, fig. 5, and Text-fig. 4 E, presents all the zones characteristic of the main promeristem. Compared with the stage of development illustrated in Pl. **20**, fig. 4, and Text-fig. 4 D, both the file and flank meristem zones have increased considerably in size, and the third layer of the central initiation zone is mainly responsible for these increases.

The prophylls of the buds are initiated by periclinal divisions in the second tunica layer and, up to this initiation, no procambium is found in the bud. At the formation of the prophylls (Pl. **20**, fig. 6), two procambium strands form in the flank meristem of the bud in connexion with the foliar emergences. These two strands of provascular meristem, at their formation, have no connexion with either the vascular system of the subtending leaf or the vascular system of the main axis. It has, however, been observed, from an examination of numerous series of sections, that, as the bud grows, its two procambium strands develop basipetally into the main axis there to merge with the two traces of the subtending leaf.

Inflorescence development

The marked transition from the vegetative rosette to the actively growing inflorescence in *Arabidopsis* and *Capsella* is not to be found in *Anagallis*. As has been described, the *Anagallis* vegetative shoot is a structure that grows actively in length and, when it enters the reproductive phase, it changes only in that flower buds replace the axillary vegetative buds. Pl. **21**, fig. 1, is of a longitudinal section through the reproductive shoot of *Anagallis*, the second and fourth pairs of leaves having been cut medianly. The flower buds are shown best in the axils of the second pair of leaves. The outstanding difference between the development of axillary primordia in vegetative and reproductive shoots is that, in the latter type of shoot, the buds quickly become conspicuous protuberances because, as has been described previously, the axillary bud primordia of the second pair of leaves of the vegetative shoot are small nests of meristematic cells not elevated above the surface of the plant.

The main promeristem of the reproductive shoot, apart from being more rounded, is essentially similar to that of the vegetative shoot. A biseriate tunica is present all through the course of a plastochrone and the cytohistological zonation into central initiation, flank meristem and file meristem zones is also shown. Each leaf of the reproductive shoot receives two traces as in the vegetative shoot so that a developing internode, in transverse section, presents four procambium strands.

Flower primordium

Pl. **21**, fig. 2, and Text-fig. 4F, are of a longitudinal section illustrating the initiation of a flower primordium in *Anagallis*. The two leaf primordia shown are the youngest pair on the reproductive shoot, and flower primordia, in different stages of development, are subtended by these developing leaves. In the axil of the foliar primordium, on the right, a flower primordium at the initiation stage is to be observed. This meristematic zone, that will later form a flower bud, is delimited from the main promeristem by a sector of compressed, dense cells and has been formed in the flank meristem zone of the apex. It is itself about three layers of cells deep and shows a biseriate tunica which is derived from that of the main promeristem. The developing flower bud, in the axil of the foliar primordium on the left, is further advanced, and now bulges above the apex surface, but the biseriate tunica is still evident.

Following initiation, the development of the flower primordium is very rapid, and Pl. **21**, fig. 3, shows one of these structures at the second node. The emergence is enclosed within a mantle of dense cells, about four layers deep, and a two-layered tunica is present in the flat apex of the primordium, but the second layer of the zone has been disturbed by periclinal divisions on the right to initiate a sepal primordium. The core of the developing flower is formed of highly vacuolate cells which show active transverse divisions and which resemble the file meristem of the vegetative apex. As far as can be made out, these cells originate from the third layer of meristematic cells from the surface of the flower primordium.

Text-fig. 4G shows an *Anagallis* flower primordium at stamen initiation, periclinal divisions in the second tunica layer being responsible for the formation of these flower parts. The pedicel has been differentiated from the receptacle, and its central vacuolated cells are undergoing extremely active transverse divisions. Two procambium strands are to be seen in this basal part of the flower primordium. The receptacle with its developing sepals and initiated stamens has also undergone a certain amount of vacuolation and, in fact, the only remaining dense meristematic region of the apex is the biseriate tunica.

Gynaeceum initiation is shown in Text-fig. 4H. The placenta is exposed at this stage of flower development and its two surface layers exhibit a dense, meristematic appearance. The lower of these surface layers seems to be involved in the production of cells which quickly vacuolate and undergo active transverse divisions. These files of dividing cells are responsible for the vertical growth of the placenta and, around the placenta, the ovary wall is beginning to develop. Text-fig. 4 H also shows the acropetal growth of procambium from one of the pedicel strands to one of the sepal primordia.

As in *Arabidopsis* and *Capsella*, corolla development is retarded in *Anagallis*. Pl. 21, fig. 4, is of a longitudinal section of a flower bud where all the parts, apart from the corolla, are more or less fully formed. However, two petal primordia are shown that are obviously far behind the rest of the flower parts in development. The petal primordium, on the left, exhibits a well-marked apical meristem. An interesting feature, illustrated by Pl. **21**, fig. 4, is the acropetal development of procambium to the placenta of the gynaeceum from one of the pedicel strands. Pl. **21**, fig. 5, is taken from the same series of sections as Pl. **21**, fig. 4, and shows how, from the same pedicel strand mentioned in the previous sentence, procambium develops acropetally into a sepal, petal and stamen.

Although the corolla does not mature until some time after the stamens and gynaeceum, its initiation is to be observed at quite an early stage in flower development. Pl. **21**, fig. 6, is a median longitudinal section of a flower bud at the time of gynaeceum initiation. A slight bulge, to be seen at the base of the left stamen primordium, is the first indication of corolla formation. Its surface cells show active anticlinal divisions, while the subjacent cells have enlarged considerably.

It has already been shown (Text-fig. 4 G) that two procambium strands are present in the *Anagallis* flower pedicel and, also, that procambium develops acropetally from these strands into the flower parts (Text-fig. 4 H, Pl. **21**, figs. 4, 5), but no mention has been made of the relationship between the pedicel procambium and that of the reproductive shoot. Flower bud primordia, in all stages of development, have been examined, and it has been demonstrated conclusively that the two pedicel provascular meristem strands develop acropetally from the traces of the subtending leaf, one from each trace, into the developing flower primordium.

Comparison of axillary vegetative and flower buds

A comparative study of the axillary vegetative and flower buds of *Anagallis* provides some interesting information. The outstanding difference between floral and vegetative buds, in their early stages of development, is the more rapid enlargement of the flower bud. This type of bud is usually quite conspicuous at the second node, whereas the axillary vegetative buds do not become prominent until the third or fourth node.

However, there are many features common to the early development of these axillary structures. Both are detached portions of the main apical meristem, and both are delimited from this promeristem by zones of compressed cells. Each detached portion, no matter whether it will later give rise to a vegetative or a flower bud, consists of part of the three surface layers of flank meristem of the main promeristem which includes a biseriate tunica. The double tunica persists during the early development of both types of bud, and vertical growth is from a file meristem produced initially by the third layer of flank meristem. The development of all buds is essentially the same up to the stage where they protrude above the plant surface and consist of a mantle of about four layers of meristematic cells enclosing a central core of vacuolating file meristem (Pl. **20**, fig. 5, Text-fig. 4 E and Pl. **21**, fig. 3).

After this, the trend of development varies. In the vegetative bud, two foliar primordia are initiated in the flanks of the structure by periclinal divisions in the second tunica layer, and then the central part of the apex of the bud begins to function as the central initiation zone in the promeristem of the main leafy shoot producing file meristem basally and foliar foundations with their emergences laterally. However, no central initiation zone becomes established in the flower bud and, instead, its whole apical meristematic region is given over to the initiation of flower parts, the gynaeceum being terminal, Vacuolation takes place very rapidly in the future flower receptacle to leave a dense.

meristematic biseriate tunica, in the second layer of which are initiated the flower parts. This initiation is similar to the initiation of the foliar primordia of the axillary vegetative buds.

Both types of bud possess two procambium traces from which procambium develops acropetally into the foliar primordia of the vegetative bud and acropetally into the flower part primordia of the reproductive bud. However, although it has been shown that, in the vegetative bud, the two traces develop in association with the first pair of leaves and then grow basipetally to join the traces of the subtending leaf, in the case of the flower bud, the bud traces always develop acropetally from the existing traces of the subtending leaf.

Conclusions and discussion

The research that has been carried out into the structure and growth of the growing points of the main vegetative axes of *Arabidopsis*, *Capsella* and *Anagallis* shows conclusively that the tunica-corpus concept can well be applied to these apices, as it has been applied in many other dicotyledonous plants.

Popham (1951) has defined the tunica as a zone in whose cell layers no periclinal divisions occur except at leaf or bud initiation. During the present investigation, the tunica depth has only been considered in the growing vegetative apex in relation to leaf formation, for it has been found, at least in *Anagallis*, that the tunica, characteristic of the main promeristem, is retained at bud initiation. Also, as far as the material has been suitable, the tunica depth has been traced throughout the course of a plastochrone. *Anagallis*, with its opposite and decussate phyllotaxis, proved most suitable for this type of investigation.

Longitudinal sections of *Anagallis* vegetative apices at all stages of the plastochrone have been examined, and the number of surface cell layers showing no periclinal divisions, except at leaf initiation, ascertained. As has been described previously, the number of cell layers in this plant is characteristically two. The vegetative tips of *Arabidopsis* and *Capsella*, with their alternate phyllotaxis, proved more difficult material in which to study tunica depth through the growth period. In the case of *Arabidopsis*, the apex was studied at various stages of the plastochrone and the tunica appears to be biseriate in this plant, the second layer, as in *Anagallis*, being disturbed at leaf initiation. The growing point of *Capsella* was not studied in sufficient detail to provide accurate information on tunica depth.

It is hardly possible to draw wide conclusions of the phylogenetic significance of the tunica depth from a study of the vegetative apices of three plants from two widely separated families of dicotyledonous plants, but the biseriate tunica appears to be quite common in this group of Angiosperms. Popham (1951) has listed the tunica depth recorded for about fifty Dicotyledons, and this zone is said to consist of two layers of cells in half of these plants. A perusal of the many papers on stem apex morphology has shown that, quite commonly, an investigator draws his (or her) conclusions on tunica depth from a growing point at one stage of the plastochrone, and also includes in this zone cell layers which show occasional periclinal divisions, apart from those concerned with leaf initiation. This random assessment of tunica depth seems to be quite unjustified and, for this reason, it is suggested that many of the published statements concerning the number of cell layers in this surface zone are without very much significance. Most notice should be taken of those workers who have studied the depth of the tunica, in its strict sense, throughout the entire course of a plastochrone (Cross & Johnson, 1941) and those (Satina, Blakeslee & Avery, 1940; Dermen, 1945, 1947), who have employed induced periclinal chimeras in their investigations. There has, unfortunately, been comparatively little research carried out on these lines, and the plants studied have been chosen from widely differing families. However, it is significant that, as far as can be ascertained, the tunica in these plants is always biseriate and it may well be that a double-layered surface zone is characteristic of the vegetative apices of all dicotyledonous plants. Some workers (Cross, 1937; Reeve, 1948) have reported fluctuations in the depth of the tunica during growth. These observations have not been confirmed during the present investigation.

The tunica-corpus concept has been elaborated in later years by a consideration of the cyto-histological zones present in the apex. This zonation, based on the nature of the cell contents rather than on the disposition of the cell walls, was first applied to certain Gymnosperms, but has now been used in descriptions of many Angiosperm apices. It is of great value in interpreting the corpus of the apex, but it does not supersede the original concept of Schmidt (1924). Rather, these two interpretations should be used in conjunction with each other, and together they afford a reasonable understanding of the anatomical and histological processes of a growing vegetative apex.

Central initiation, flank meristem and file meristem zones have been found in the vegetative apices of *Arabidopsis*, *Capsella* and *Anagallis*, and, in these three genera, the zones perform exactly the same functions. The flank meristem produces the epidermis, cortex, procambial system and leaves of the plant, while the file meristem produces the pith. The central initiation zone is the self-perpetuating region of the apex.

Again, a study of the growing point, throughout the course of a plastochrone, is necessary for a full understanding of the establishment and significance of these zones. This has been done only for *Anagallis*. The apex of this plant, at minimal area, is quite flat and appears to show, in longitudinal section, three surface layers of dense, meristematic cells and a fourth layer of irregularly arranged cells of a similar nature. This meristematic region, at least the three surface layers, constitutes the central initiation zone. As the apex enlarges prior to the formation of the next pair of leaf primordia, cells are cut off from the sides of this zone and also from its basal region.

Those cells, cut off from the sides of the central zone, form the surrounding flank meristem. The two-layered tunica is maintained during this cell production, but the cells produced by the third layer of the central initiation zone soon undergo numerous periclinal divisions to increase the depth of the flank meristem to about four or five layers of cells. As many authors have stated for other plants, these surrounding flank meristem cells stain more deeply with protoplasmic stains than the central cells. The same statement applies to *Arabidopsis* and *Capsella*.

In *Anagallis*, during the enlargement of the apex, the cells cut off from the base of the central zone, vacuolate and enlarge to undergo repeated transverse divisions to form typical file meristem. It is the activity of this zone that produces growth in length to form finally the large dome-shaped apex prior to the initiation of the next pair of leaf primordia. The work of Satina *et al.* (1940) and Cross & Johnson (1941) has shown that divisions in various planes in the third layer of the apex are responsible for the establishment of the corpus in the apices of the plants they studied. The observations now presented for *Anagallis* support this idea, and it is highly likely that the fourth layer of irregularly arranged cells to be observed in the apex just after leaf initiation is the first sign of file meristem production, and it is not strictly part of the central initiation zone. Dense cells, transitional between those of the central initiation zone and the typical vacuolate file meristem, have been observed in *Arabidopsis* and they have been described as forming a cambium-like zone (Vaughan, 1952*a*). A similar observation has been made by Ball (1941), Majumdar (1942), Philipson (1946) and Popham & Chan (1950). The claim made by the last pair of authors that the presence or absence of this intermediate zone is related to apex size has been disputed (Vaughan, 1952*a*).

In *Anagallis*, the file meristem can be followed for some distance behind the actual apex through a number of nodes and internodes, its cells enlarging in a longitudinal direction and undergoing divisions, mainly in the transverse plane. This high rate of cell activity is in contrast to the state of affairs in *Arabidopsis* and *Capsella* where the file meristem is of very limited development, its cells undergoing little longitudinal enlargement and very quickly passing over into typical pith cells. This difference in the activity of the file meristem in the plants studied is obviously related to the different growth forms, for the leafy shoot of *Anagallis* is an actively elongating structure with well-marked internodes, whereas both *Arabidopsis* and *Capsella* are typical rosette plants, with very short internodes.

Procambium development has been studied in the vegetative promeristems of *Arabidopsis*, *Capsella* and *Anagallis*. It has been found that procambium is always formed in relation to leaf initiation, and that the development of this tissue to the leaves of the plants under consideration is continuously acropetal. These observations are in accordance with the views of most recent workers (Majumdar, 1942; Esau, 1942; Philipson, 1949; Vaughan, 1952*b*).

The study of the initiation and development of the axillary vegetative buds of *Anagallis* has provided a certain amount of useful information. This aspect of developmental morphology has recently been reviewed by Philipson (1949) and Gifford (1951).

Whether bud primordia originate as residual portions of the apical meristem or by divisions of previously vacuolate cells is a matter of opinion. Support for the first view has been given by Louis (1935), Miller & Wetmore (1946), Philipson (1948) and Gifford (1951), but Majumdar & Datta (1946) report that bud primordia develop from vacuolate cells in the leaf bases in *Heracleum* and *Leonurus*. As far as *Anagallis* is concerned, the buds definitely originate as detached portions of the main promeristem and, as such, can always be recognized at the second or third nodes. It has been shown that these primordia become delimited from the apical meristem by a zone of compressed cells. This zone has been recognized by Gifford (1951), and has been described by Schmidt (1924) as the 'shell zone'. It is thus seen that the origin of buds in *Anagallis* agrees with the type of development described by most workers, and one might assume that this ontogentical process may follow a similar course in all vascular plants for Wardlaw (1943) has shown that the buds of certain ferns originate as persistent portions of the apical meristem.

It is of interest to note that, in *Anagallis*, the axillary bud primordia, when isolated by the vacuolation of the surrounding tissues, consist of three layers of dense, meristematic cells. The two surface layers of the primordium form a definite tunica, which is obviously derived from the biseriate tunica of the main promeristem. The cells of this bud tunica undergo only anticlinal divisions during the next stages of growth. The cells of the third layer of the primordium, on the other hand, undergo both anticlinal and periclinal divisions to produce, laterally, the third and fourth layers of the flank meristem and, basally, the actively dividing cells of the file meristem. The activity of the third layer of meristematic cells now described corresponds closely with the type of activity suggested previously for the third layer of cells of the central initiation zone of the main promeristem, and it is clear that bud primordium development in *Anagallis* really involves the establishment of a growing point similar to the main apical meristem.

Variance of opinion is also shown concerning the development of the procambium traces of axillary vegetative buds. Some authors have stated that the bud traces develop acropetally from the procambium of the main axis into the developing bud (Louis, 1935; Reeve, 1943; Miller & Wetmore, 1946; Philipson, 1948; Garrison, 1949), while others claim basipetal development for the traces before a union is made with the vascular system of the main axis (Majumdar & Datta, 1946; Gifford, 1951). It has been shown for *Anagallis* that the two bud traces arise in conjunction with the first pair of leaves and then develop basipetally to join the leaf traces of the subtending leaf. This corresponds with the observations of Ball (1952) on the isolated apex of *Lupinus* for, in a way, the detached bud primordium of *Anagallis* is similar to the experimentally produced isolated apex of *Lupinus*. Ball (1952) found that the procambium produced in the partially detached promeristem developed basipetally to join the vascular system of the main axis and that, until this union was complete, active vertical growth of the apex did not begin. A similar state of affairs is shown by the axillary buds of *Anagallis*, because active branch development certainly does not start until the traces of the bud and of the subtending leaf have united.

The developmental anatomy of the change from the vegetative to the reproductive phase in flowering plants is a matter of some importance and, therefore, the development of the inflorescence in *Arabidopsis*, *Capsella* and *Anagallis* has been studied as carefully as possible. To relate the information that has been obtained for these plants to that obtained by previous workers, it would seem necessary to consider briefly the general morphology of their flower-bearing axes and, in doing this, it is obvious that the inflorescence units of *Arabidopsis* and *Capsella* differ markedly from that of *Anagallis*. *Arabidopsis* and *Capsella* resemble each other in that the truly vegetative parts of the plants are in the form of rosettes. The main inflorescence axis, in both types, normally develops directly from the rosette axis and grows vigorously in a vertical direction to produce laterally a few cauline leaves and then numerous flowers. In *Anagallis*, on the other hand, the inflorescence differs from the vegetative shoot only in that flower buds replace vegetative buds.

As far as is known, no work has been published relating to inflorescence development in the Cruciferae, but the researches of Philipson (1946, 1947, 1948), Lawalrée (1948) and Popham & Chan (1952) on plants, mainly of the Compositae, with capitulum type inflorescences are of interest here. The capitulum type of inflorescence is not found in either *Arabidopsis* or *Capsella*, but the inflorescences of these Cruciferae and of those Compositae that have been studied share one common relationship in that they both differ markedly in morphological form from the vegetative axes that bear them. Accordingly, one would expect certain common features of development.

Both Philipson (1946) and Lawalrée (1948) claim that one of the first signs of inflorescence initiation in the plants they studied is elongation of the dense cells of the vegetative promeristem and of the subjacent vacuolating cells, but Popham & Chan (1952), who studied *Chrysanthemum* plants grown under carefully controlled photoperiodic treatment, state that the processes of cell enlargement and active cell division in the file meristem zone of the apex are responsible for the inflorescence initiation. The results now presented for *Arabidopsis* and *Capsella* agree with the views of the last-named authors. During inflorescence initiation in these plants, there is no obvious elongation of either the central initiation zone cells or the flank meristem cells, but the file meristem cells certainly enlarge in a longitudinal direction and undergo repeated transverse and longitudinal divisions. This file meristem activity is so rapid that the young inflorescence appears as a dome-shaped structure with flank meristem running down its sides. Similar observations have been made by Philipson (1946) and Popham & Chan (1952).

A point of difference, however, between inflorescence development in the Cruciferae and the Compositae that have been studied concerns the persistence or disappearance of the central initiation zone of the apex. In both *Arabidopsis* and *Capsella*, and in the various Compositae that have been described by other authors, the central initiation zone is present in the apex of the young inflorescence. However, in the last-named group of plants, as the inflorescence primordium differentiates into pedicel and receptacle and the floret primordia are formed, the central initiation zone is lost and is replaced by flank meristem (Philipson, 1946; Popham & Chan, 1952). In *Arabidopsis* and *Capsella*, the central initiation zone persists in the inflorescence apex at all stages of development of the flower-bearing axis.

It would not be wise, until many more inflorescence types have been described in terms of the cyto-histological zonation concept, to make a definite statement on the importance of the persistence of the central initiation zone now described, but it is highly probable that there is a correlation between the persistence or disappearance of this zone and the habit of the inflorescence in the apex of which it is found. The capitulum of the Compositae is a structure of determinate growth, the florets soon occupying the summit of its receptacle, whereas the raceme of *Arabidopsis* and *Capsella* is a structure of indeterminate growth which continuously undergoes vertical growth, its apex producing lateral flower primordia. In many respects, the inflorescence apex of *Arabidopsis* and *Capsella* resembles that of any normal elongating vegetative shoot.

From the information given previously concerning the developmental anatomy of *Anagallis*, it is clear that no great morphological change takes place in the plant axis at the formation of the inflorescence. The early appearance of the flower buds, in contrast to the delayed development of the vegetative buds, has been reported by Miller & Wetmore (1946) for *Phlox*, and by Boke (1947) for *Vinca*.

It is thus seen that the inflorescence apices of *Arabidopsis*, *Capsella* and *Anagallis* are direct developments of the vegetative growing point of the plant, showing tunica zones of the same depth and a similar cyto-histological zonation. In all cases, a biseriate tunica has been recorded.

The establishment of the flower primordia and their early development have also been studied in the three plants under consideration, and certain general conclusions have been reached. In *Arabidopsis*, *Capsella* and *Anagallis*, the flower primordia are initiated by periclinal divisions in the third flank meristem layer of the main promeristem, and they all retain, during their early development, a biseriate tunica and a corpus. The retention of the double-layered tunica, characteristic of the vegetative apex, in the early flower primordium has also been described for various plants by Satina & Blakeslee (1941) and Philipson (1947, 1948). This observation indicates a close relationship between the floral apices of *Arabidopsis*, *Capsella* and *Anagallis*, and the corresponding vegetative apices.

Additional support for this statement is provided by the study of the trace system of the flower bud of *Anagallis* which closely resembles that of the vegetative bud. Acropetal development of procambium to the flower primordia of *Arabidopsis* and *Capsella* has also been described, a statement which is in accordance with the views of other workers (Miller & Wetmore, 1946; Boke, 1947; Philipson, 1948).

The views of Grégoire (1938) are well known to the student of developmental anatomy. However, in later years, his results have been much criticized, especially his opinion that reproductive and vegetative apices are totally dissimilar. It has been shown that inflorescence apices of *Arabidopsis*, *Capsella* and *Anagallis* are morphologically the same as the vegetative growing points and, also, the floral apices of these species, up to a certain stage of development, resemble vegetative promeristems. At a later stage of development, the activity of a floral apex must clearly differ from that of an ordinary vegetative apex and, as far as can be made out, the difference is the result of a central initiation zone failing to develop, the floral parts being formed in rapid succession and occupying the entire surface of the flower receptacle. The corpus does not, as in the vegetative promeristem, retain any initiating properties but undergoes complete vacuolation.

Some information has been published concerning the initiation and development of the flower parts of various plants (Newman, 1936; Grégoire, 1938; McCoy, 1940; Satina & Blakeslee, 1941, 1943; Miller & Wetmore, 1946; Lawalrée, 1948; Boke, 1948, 1949). Generally speaking, the initiation of all flower parts has been described as taking place in the second tunica layer of the flower receptacle, but Satina & Blakeslee (1941, 1943) have claimed that, in *Datura*, the initiation of the stamens and carpels takes place in the third layer of the floral apex and, accordingly, these floral parts are more axial in nature than foliar. The results that have been obtained for *Arabidopsis*, *Capsella* and *Anagallis* demonstrate that, in these plants, all the floral parts are initiated by periclinal divisions in the second tunica layer. This type of initiation is, of course, similar to that of foliage leaves, and it gives a tentative indication of the foliar nature of the flower parts. The apical and marginal growth of the sepals and petals is also very similar to that in the developing foliage leaves.

The retarded development of the corolla in *Arabidopsis*, *Capsella* and *Anagallis* is interesting, i.e. similar to that which has been observed by Miller & Wetmore (1946) in *Phlox*.

Finally, in this investigation, it has been found that procambium always develops acropetally from the pedicel into the flower parts. This is in accordance with the views of Grégoire (1938). The development of provascular meristem to the stamens and carpels is difficult to observe in their early stages, and Boke (1949), finding the same difficulty in *Vinca*, regards procambium development to the essential organs as a fairly late process. This acropetal development of procambium to the flower parts is similar to the state of affairs in developing foliar primordia and, again, this statement may be taken as a tentative indication of the foliar nature of the flower parts.

It is clear that the initiation and development of foliage leaves and flower parts have many features in common, but it would be unwise to place too great a stress on a similar homology between the two types of organs from the present evidence of developmental anatomy. It may be possible, in the future, to obtain further supporting evidence for the homology if certain techniques of the plant physiologist are combined with those of the anatomist but, at the moment, it would seem wiser to regard the floral members merely as lateral emergences concerned with reproduction.

SUMMARY

1. The structure and growth of the vegetative, inflorescence and floral apices of *Arabidopsis thaliana* (L.) Heynh., *Capsella bursa-pastoris* (L.) Medic. and *Anagallis arvensis* L. have been investigated.
2. The vegetative apices of all three plants show tunica and corpus zones and the normal cyto-histological zonation.
3. Leaf primordia are initiated by periclinal divisions in the second tunica layer of the apex, and show apical and marginal growth during their early development.
4. Leaf procambium development is always continuously acropetal.
5. In *Anagallis*, axillary vegetative buds arise as detached parts of the apical meristem and their traces develop basipetally to join the traces of the subtending leaves.
6. No marked morphological changes are to be observed in *Anagallis* during the formation of the inflorescence, but, in *Arabidopsis* and *Capsella*, marked changes have been observed and have been fully described.
7. The inflorescence apices of all three species show tunica and corpus zones and a cyto-histological zonation. It has been shown that these apices are essentially similar to those of vegetative shoots.
8. Flower primordia are initiated by periclinal divisions in the third layer of the flank meristem of the inflorescence apex.
9. Procambium development to the flower primordia is continuously acropetal.
10. The floral apex shows tunica and corpus zones.
11. All the floral parts are initiated by periclinal divisions in the second tunica layer, and procambium development to these parts is again continuously acropetal.
12 A possible homology between foliage leaves and flower parts has been discussed.
13. In all three plants, the petals are the last of the flower parts to mature.

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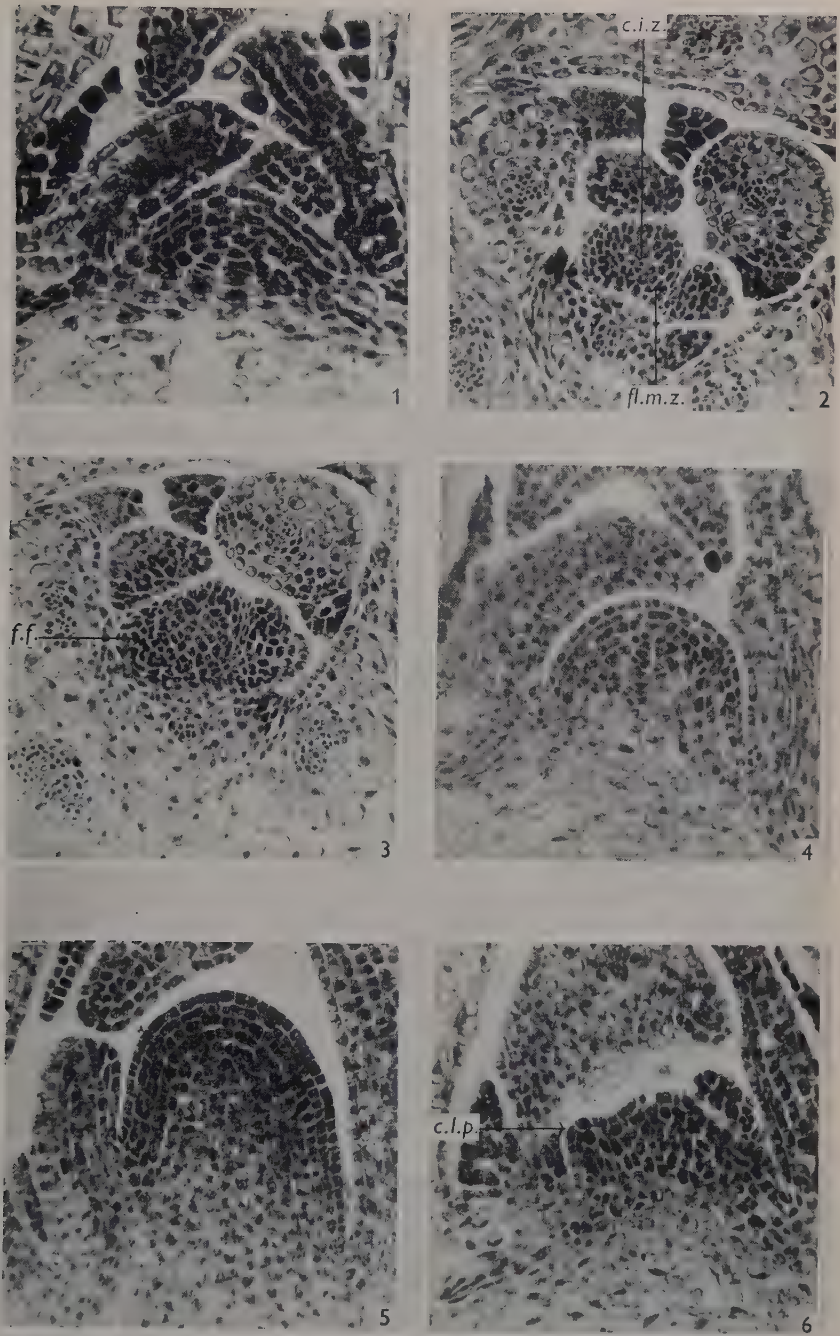
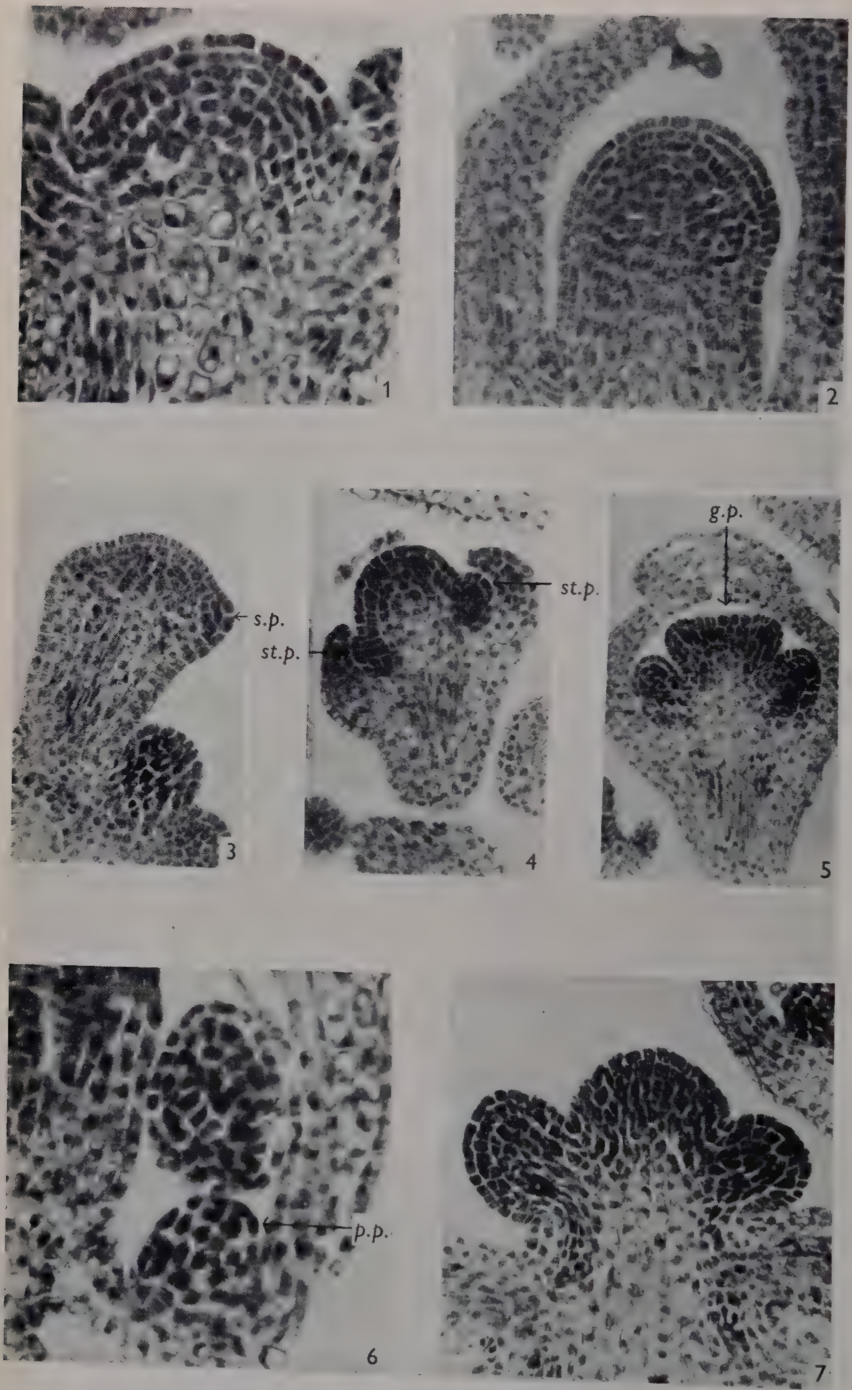
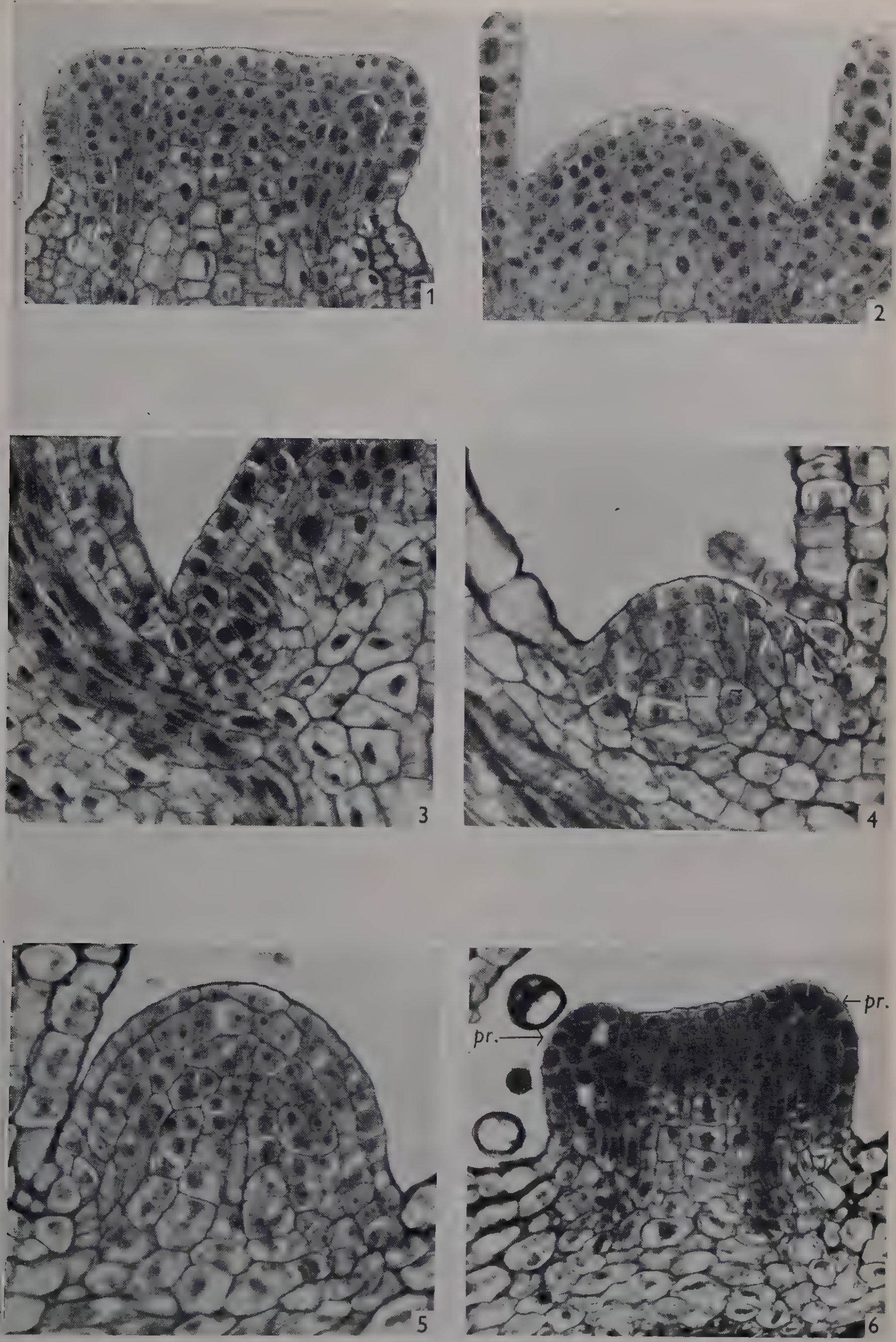


***Arabidopsis* and *Capsella* shoot apices**

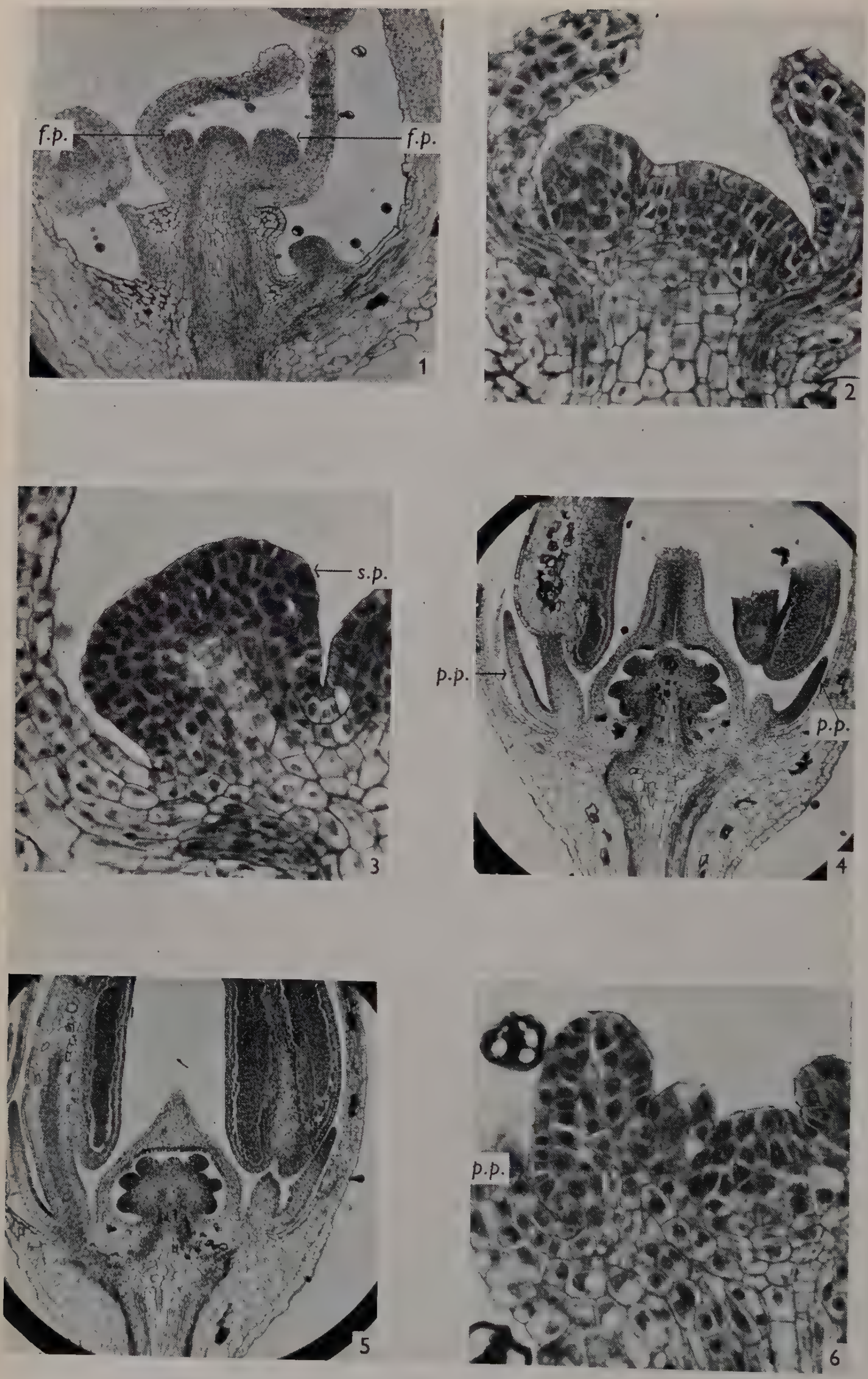
(*Facing p.* 300)



***Arabidopsis* and *Capsella* shoot apices**



Anagallis shoot apices



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EXPLANATION OF PLATES 18–21

(All photographs from untouched negatives.)

Plate 18

Fig. 1. Median longitudinal section of an *Arabidopsis* vegetative apex (× 473).

Fig. 2. Transverse section of an *Arabidopsis* vegetative apex showing the central initiation (*c.i.z.*) and flank meristem (*fl.m.z.*) zones (× 288).

Fig. 3. Transverse section of an *Arabidopsis* vegetative apex (× 288), taken just below fig. 2, showing a foliar foundation (*f.f.*).

Fig. 4. Longitudinal section showing the early initiation of the inflorescence in *Arabidopsis* (× 255).

Fig. 5. Longitudinal section showing a fairly late stage in inflorescence formation in *Capsella* (× 237).

Fig. 6. Longitudinal section showing the initiation of a cauline leaf primordium (*c.l.p.*) in *Arabidopsis* (× 255).

Plate 19

Fig. 1. Median longitudinal section of an *Arabidopsis* inflorescence apex (× 400).

Fig. 2. Median longitudinal section of an *Arabidopsis* inflorescence apex showing the initiation of a flower primordium (× 367).

Fig. 3. Longitudinal section of a *Capsella* flower primordium (× 297) showing the initiation of a sepal primordium (*s.p.*).

Fig. 4. Longitudinal section of a *Capsella* flower primordium (× 263) showing the initiation of stamen primordia (*st.p.*).

Fig. 5. Longitudinal section of a *Capsella* flower primordium (× 232) showing the initiation of the gynaeceum primordium (*g.p.*).

Fig. 6. Longitudinal section of part of an *Arabidopsis* flower primordium (× 550) showing a retarded petal primordium (*p.p.*).

Fig. 7. Longitudinal section showing the acropetal development of procambium to two young *Capsella* flower primordia (× 263).

Plate 20

Fig. 1. Median longitudinal section of an *Anagallis* vegetative apex at minimal area (× 294).

Fig. 2. Median longitudinal section of an *Anagallis* vegetative apex at maximal area (× 294).

Fig. 3. Median longitudinal section (× 425) showing a bud primordium in the axil of one of the second pair of leaves of the main vegetative axis of *Anagallis*.

Fig. 4. Longitudinal section (× 450) showing a bud primordium in the axil of one of the fourth pair of leaves of the main *Anagallis* vegetative axis. The file meristem zone is now quite well developed.

Fig. 5. Longitudinal section of an *Anagallis* axillary bud primordium which shows the cyto-histological zones characteristic of the main vegetative promeristem (× 423).

Fig. 6. Longitudinal section showing the initiation of the prophylls (*pr.*) in the *Anagallis* axillary vegetative bud (× 283).

Plate 21

Fig. 1. Longitudinal section (× 67) of the *Anagallis* reproductive shoot showing flower primordia (*f.p.*).

Fig. 2. Longitudinal section showing the initiation of flower primordia in *Anagallis* (× 282).

Fig. 3. Longitudinal section showing the initiation of a sepal primordium (*s.p.*) in *Anagallis* (× 273).

Fig. 4. Longitudinal section of an *Anagallis* flower bud with all the flower parts formed (× 48). Two petal primordia (*p.p.*) are shown.

Fig. 5. Longitudinal section of an *Anagallis* flower bud showing the acropetal development of procambium to a developing sepal, petal and stamen (× 48).

Fig. 6. Longitudinal section of an *Anagallis* flower primordium (× 319) showing the initiation of a petal primordium (*p.p.*).

The taxonomy and origins of the cultivated bananas.

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(With 2 Text-figures)

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I. INTRODUCTION

Musa acuminata Colla and *M. balbisiana* Colla are two wild species from which have originated nearly all the edible bananas. Previous work has indicated the existence of edible diploid and triploid forms of *M. acuminata*, of diploid and triploid forms of inter-specific hybrid origin and of triploid forms of *M. balbisiana* (Dodds & Simmonds, 1948*b*; Cheesman, 1947, 1948).

There are two facts that are very hard to explain on this view of the taxonomy of the cultivated bananas. One is that no edible diploid forms of *M. balbisiana* are known, though their existence (at least in past time) is a necessary assumption to explain the occurrence of edible triploid forms. The other fact is that mechanisms for the production of vigorous tetraploid bananas are well known from cytogenetic experiment and yet only one such banana is known to occur naturally. The work reported in this paper seems to solve the first problem satisfactorily but not the second. It also suggests a re-interpretation of the Linnaean name, *M. paradisiaca*.

II. MATERIALS AND METHODS

Plant material. Table 1 is an annotated list of the edible varieties used. The names given are those under which the varieties were received at the I.C.T.A.; sometimes a choice has been made when a variety was received under several different names but no attempt is made to set out the synonymy. All these varieties are unquestionably distinct from each other and known or suspected somatic mutants have been excluded. The list probably represents a fair though restricted sample of the group. Varieties marked with an asterisk (*) appear to be particularly widely spread and important. Names given in inverted commas were probably invented for use in museum collections of bananas.

Taxonomic methods. The fifteen characters shown in Table 2 were selected as being most useful for diagnostic purposes. In sum they differentiate reliably between *M. acuminata* and *M. balbisiana*, even though few of them individually suffice to separate the two species with certainty. Each character was scored on a scale from one (typical *M. acuminata*) to five (typical *M. balbisiana*); the possible range of total scores was therefore 15 to 75. Some diagnostic characters of the male bud are shown in Fig. 3 and other figures are given by Dodds & Simmonds (1948*b*).

III. RESULTS

Results are set out in Appendices 1–3 and summarized in Table 3. Expected scores have been calculated on the assumption that they are proportional to the relative genetic contributions of the two species and that, in sporogenesis, random assortment of chromosomes occurred. Then, if a and b ($a+b=1$) are the respective contributions of *M. acuminata* and *M. balbisiana*, if S_A and S_B are the scores of the same 'pure' species, and S the score of a plant under investigation:

$$\begin{aligned} S &= S_A + b(S_B - S_A) \\ &= aS_A + bS_B. \end{aligned}$$

The limiting scores, 15 and 75, have been used for S_A and S_B.

Table 1

Variety (in order given in Appendices)	Sources	I.C.T.A. type no.	Notes
*Sucrier	Trinidad, etc.	19	—
Palembang	Trinidad	21	—
*Bande	Trinidad, etc.	22	—
Pisang Lilan	Malaya	32	—
Tongat	N. Borneo	33	—
Sikuzani	Zanzibar	38	—
Paka	Zanzibar	39	—
Mjenga Maua	Zanzibar	40	—
'Small Type'	Uganda	41	—
*Ney Poovan	S. India, B.W.I.	20	—
*Gros Michel	Trinidad, Malaya, etc.	1	The 'Jamaica banana'
*Masak Hijau	Malaya, etc.	5	The Lacatan of Jamaica, tallest member of the Cavendish group
*Green Red	Trinidad, Malaya, S. India, etc.	7A	The Red Banana (a chimaera) is excluded
'Rio'	Brazil	10	—
'Orotava'	Canary Islands	8	—
Maruthuva	Ceylon, Siam, B.W.I.	16	—
Rajah	Malaya	18	—
Palimbang	N. Borneo	34	Note spelling and cf. Palembang above
Gitigi	Kenya	42	—
Mutika	Kenya	43	Probable mutants excluded
Lujugira	Uganda	44	—
Nambi	Uganda	45	—
Kitarasa	Tanganyika	46	—
Lwekilo	Tanganyika	47	—
Ntobe	Tanganyika	48	—
Mysore	S. India, Burma, B.W.I.	6	—
King	Trinidad, N. Borneo	13	—
Celat	British Guiana	14	—
Pome	Orotava, Madras, etc.	15	—
Nadan	Madras	29	—
Nendra Padaththi	Madras	30	Rajapuri (a probable mutant) excluded
*Silk	S. India, Malaya, B.W.I.	17	Probably the type of *M. sapientum* L.
*Horn Plantain	B.W.I., etc.	23	Various mutants excluded
*French Plantain	B.W.I., etc.	24	Probably the type of *M. paradisiaca* L.
Grindy	B.W.I.	35	—
Sept-semaines	Martinique	36	—
*Bluggoe	B.W.I., Africa, etc.	11	—
Awak Legor	Malaya	12	—
Peyan	Madras	27	—
Ney Mannan	Madras	28	—
Pacha Bontha Bathees	Madras	31	—
Tiparot	Philippines via Honduras and Jamaica	37	—

Taking the contents of Table 3 in order, the following facts are apparent:

(1) Diploid *M. acuminata*, whether seeded or edible, is consistently slightly higher than the limiting score of 15, and wild diploid *M. balbisiana* slightly less than the other limit, 75.

(2) Diploid F_1 hybrids agree well with expectation and with hybrid group I. This group contains only one plant, Ney Poovan, which was described and figured in some detail by Dodds & Simmonds (1948*b*) under the label Type 20.

Table 2

Character	*M. acuminata*	*M. balbisiana*
Pseudostem colour	More or less heavily marked with brown of black blotches	Blotches very slight or absent
Petiolar canal	Margin erect or spreading, with scarious wings below, not clasping pseudostem	Margin inclosed, not winged below, clasping pseudostem
Peduncle	Usually downy or hairy	Glabrous
Pedicels	Short	Long
Ovules	Two regular rows in each loculus	Four irregular rows in each loculus
Bract shoulder*	Usually high (ratio $< 0{\cdot}28$—Fig. 1)	Usually low (ratio $> 0{\cdot}30$—Fig. 1)
Bract curling†	Bracts reflex and roll back after opening (Fig. 1)	Bracts do not reflex (Fig. 1)
Bract shape	Lanceolate or narrowly ovate, tapering sharply from the shoulder (Fig. 1A)	Broadly ovate, not tapering sharply (Fig. 1B)
Bract apex	Acute (Fig. 1A)	Obtuse (Fig. 1B)
Bract colour	Red, dull purple or yellow outside; pink, dull purple or yellow inside	Distinctive brownish-purple outside; bright crimson inside
Colour fading	Inside bract colour usually fades to yellow towards the base	Inside bract colour usually continuous to base
Bract scars	Prominent (Fig. 1A)	Scarcely prominent (Fig. 1B)
Free tepal of male flower	Variably corrugated below tip (Fig. 1A)	Rarely corrugated (Fig. 1B)
Male flower colour	Creamy white	Variably flushed with pink
Stigma colour	Orange or rich yellow	Cream, pale yellow or pale pink

* Measured as the ratio of the vertical distances from base to broadest point and from base to apex (Fig. 1, x/y).

† In varieties with non-deciduous male bracts curling is weak or absent, regardless of genotype.

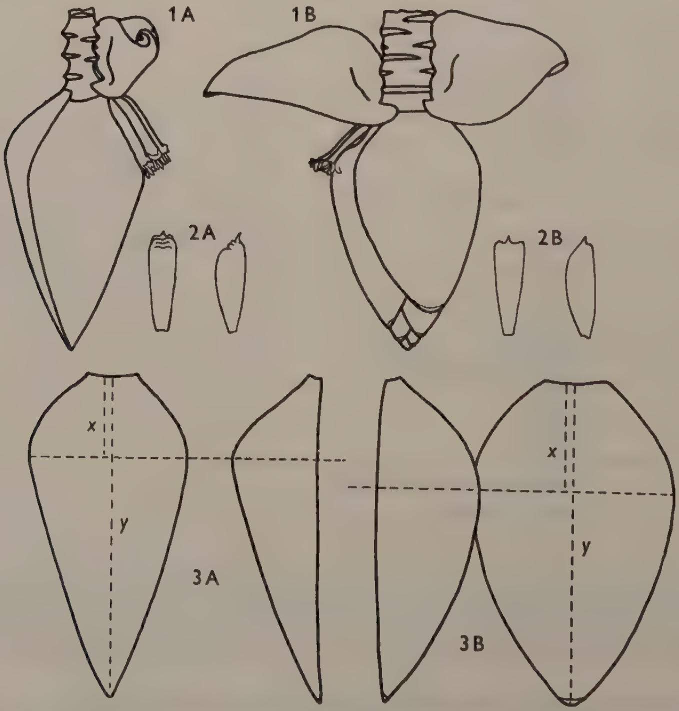

Fig. 1. Diagnostic characters in the male bud. A, *M. acuminata* B, *M. balbisiana*. 1: male buds, showing differences in shape, bract curling and bract scars (× $\frac{2}{9}$). 2A, 2B, free tepals of male flowers, showing differences in corrugation (× $\frac{1}{2}$); 3A, 3B, bracts, showing differences in shape (bract shoulder ratio $= x/y$) (× $\frac{1}{3}$).

(3) Information on an undescribed species of banana from Assam is included in this table. It is quite closely related to *M. acuminata*, crosses very readily with *M. balbisiana* and has orange-yellow flowers, a colour so far unknown in *M. acuminata* and *M. balbisiana*. Certain edible bananas (see below) have flowers of a similar colour, and on these grounds the possibility must be considered that the Assam species has contributed to the origin of the edible bananas.

Table 3. *Interpretation of taxonomic scorings*

Class	Ploidy	Constitution	No. of clones	Scores	
				Observed	Expected
M. acuminata—wild	$2x$	*AA*	20	21·0	15
M. acuminata—edible	$2x$	*AA*	9	19·6	15
M. balbisiana—wild	$2x$	*BB*	16	68·7	75
F_1 hybrids—experimental	$2x$	*AB*	11	45·9	45
Hybrid I—natural	$2x$	*AB*	1	48·5	45
Musa sp. (Assam)	$2x$	*RR*	3	32·1	—
M. acuminata—natural	$3x$	*AAA*	15	17·5	15
Hybrid II (1)—natural	$3x$	*AAB*	7	36·7	35
Hybrid II (2)—natural	$3x$	?*AAB*	4	41·6	35
		?*ARB*	4	41·6	40·7
Hybrid II (1)—experimental	$3x$	*AAB*	3	33·2	35
Hybrid III—natural	$3x$	*ABB*	5	60·4	55
Hybrid III—experimental	$3x$	*ABB*	3	59·0	55
M. acuminata—experimental	$4x$	*AAAA*	3	17·5	15
Hybrid IV—experimental	$4x$	*AAAB*	5	29·9	30
Hybrid V—experimental	$4x$	*AABB*	3	46·0	45
Hybrid VI—natural	$4x$	*ABBB*	1	67·0	60
Hybrid VI—experimental	$4x$	*ABBB*	2	64·5	60

(4) Triploid *M. acuminata* agrees well with expectation.

(5) Hybrid group II–1, natural and experimental, agrees well with expectation. The natural members are thought to have arisen by *acuminata*-backcrossing of diploid F_1 types in which restitution occurred ($AB+A \rightarrow AAB$) and/or by crossing of edible diploid *M. acuminata* (with restitution) by *M. balbisiana* ($AA+B \rightarrow AAB$). Hybrid group II-2 is the group with orange-yellow flowers referred to in (3), above. Its score is rather high but agrees well with the supposition that the Assam species has contributed a genome. This suggestion rests solely on flower colour; there is nothing else to connect the Assam species with the edible bananas and, if orange-yellow flowers were found in *M. acuminata* or *M. balbisiana*, the suggestion would be completely vitiated. At present we can only point to the possibility as a basis for future investigations.

(6) Hybrid group III represents the other backcross of the diploid F_1 hybrid (female, with restitution) by *M. balbisiana* ($AB+B \rightarrow ABB$). The natural and experimental plants agree well but both have slightly higher scores than expectation; *M. balbisiana* seems to have made a disproportionate contribution (cf. below). This group contains the bananas which have been treated previously as edible triploid forms of *M. balbisiana*. Recognition of its hybrid origin means that no pure *balbisiana* edible types are now known (see Discussion).

(7) Tetraploid *M. acuminata* agrees well with expectation, as did triploids and diploids; there is, evidently, no effect of polyploidy *per se* on score.

(8) Hybrid groups IV and V are purely experimental, no naturally occurring plants of these constitutions being known. Hybrid group V, it will be noted, agrees also in score with the diploid Hybrid group I. It has the constitution *AABB* and is therefore amphidiploid.

(9) Hybrid group VI includes the only known natural tetraploid banana, Tiparot, which agrees well with its experimental counterparts, though all have a score somewhat

greater than expectation; i.e. the group diverges towards *M. balbisiana* as did hybrid group III ((6), above). This divergence may reflect the choice of diagnostic characters or of the scale adopted—it could presumably be reduced by means of a suitable non-linear scale. Another possibility is that multiplicative action of *M. balbisiana* genes occurs and produces superficially the same effect as an error of scaling. Whatever the cause, the deviations seem to be less significant than the general agreement with expectation of the data as a whole.

The general conclusion is that the edible bananas of the section Eumusa have originated primarily from *M. acuminata* by the joint processes of hybridization with *M. balbisiana*, followed by backcrossing to both parents, and polyploidy. A minor contribution from a third species to the origins of one group of hybrids cannot be excluded as a possibility, a possibility which is yet insufficiently understood to be worth discussion in the following paragraphs.

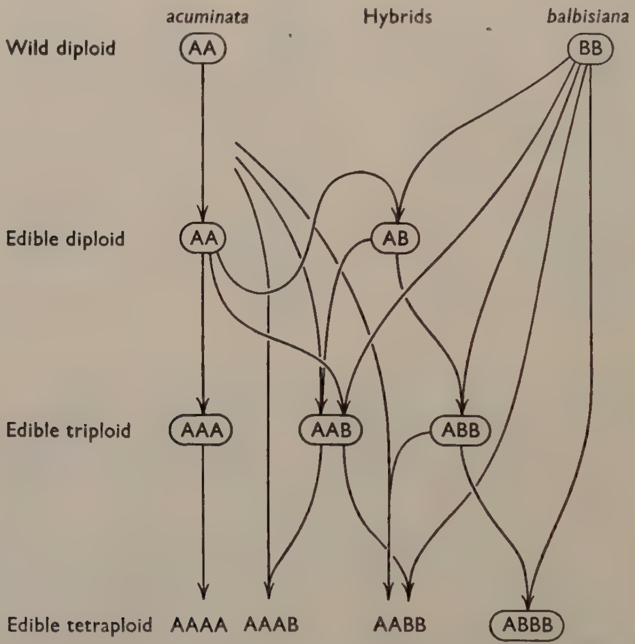

Fig. 2. The evolution of the banana complex. A, *M. acuminata*; B, *M. balbisiana*. Genotypes known to occur naturally are encircled, those known only from experiment are not. Origins from diploid *M. acuminata* in which the parent might have been either wild or edible are shown as lines of indefinite origin. Crossing of tetraploid by diploid as a source of triploids has been neglected because natural tetraploids are very rare; many triploids have been made experimentally in this fashion, however.

IV. Discussion

Evolution. It is suggested that there have been five main stages in the evolution of the banana complex (see diagram, Fig. 2).

(1) The evolution of parthenocarpy and sterility in diploid *M. acuminata*. Malaya appears to have been the most important though not necessarily the only area in which this occurred (Dodds, 1943; Dodds & Simmonds, 1948*a*; Simmonds, 1953*a*). There is no evidence that parthenocarpy also evolved in *M. balbisiana*.

(2) Outcrosssing of edible diploids of *M. acuminata* to wild *M. acuminata* and *M. bal-*

bisiana followed by human selection among the parthenocarpic products of such crosses. New *acuminata* diploids and F_1 hybrid diploid types (hybrid I) would result.

(3) The occurrence of triploidy as a consequence of haploid pollination of diploid female cells. The cytological mechanism was probably a second division restitution which is known to occur widely in *Musa* (Dodds & Pittendrigh, 1946; Dodds & Simmonds, 1946), but the occurrence of occasional first division restitutions cannot be excluded as a possibility. There is evidence of the occurrence of suitable restitutions in *M. acuminata* and in hybrids but not in *M. balbisiana*. On this basis there are four possible combinations yielding three distinct products, thus:

Female cells		Male cells	Products
AA	×	A	AAA (*acuminata* triploids)
AA	×	B	AAB (hybrid II)
AB	×	A	AAB (hybrid II)
AB	×	B	ABB (hybrid III)

The hybrid group III contains bananas treated previously as triploid forms of *M. balbisiana*. Recognition of the hybrid origin resolves the problem mentioned in the Introduction: no pure *balbisiana* edible triploids occur, and therefore the existence of edible diploids of this species need not be assumed.

The preponderance of triploids among the edible bananas doubtless reflects their superiority to diploids in respect of vigour and fruit size (Simmonds, 1948, 1952, 1953*b*).

(4) The occurrence of tetraploidy, most probably as a consequence of restitution in triploids followed by haploid pollination. Only one naturally occurring tetraploid is known; it has been shown above to be of $ABBB$ type (hybrid VI) and thus it probably arose from pollination of hybrid III by *M. balbisiana* ($ABB+B \rightarrow ABBB$). Experimental pollination of triploids has now yielded thousands of tetraploids. They were mostly vigorous plants and, when their chromosomes were counted, were found in the great majority of cases to have exactly 44 chromosomes (Cheesman & Dodds, 1942; Larter, 1948). This suggests that the restitution that gave rise to them was virtually always of the first division type, because the second division restitution characteristic of diploid hybrids of *Musa* (Dodds & Simmonds, 1946) cannot, in a triploid, give balanced gametes with exactly 33 chromosomes (or can only do so by an excessively unlikely cytological mechanism).

Tetraploids in general are vigorous (Simmonds, 1948, 1952) and are readily produced by pollination of triploids—indeed the banana breeding programme which seeks to replace the disease-susceptible Gros Michel by resistant tetraploids rests on these facts. They would be expected to occur naturally in considerable numbers and their at least apparent rarity cannot be explained at present. If more are found, they may be expected to fall into the groups defined above on the basis of experimentally produced plants. They would, incidentally, provide in nature (as they have provided in experiment) an abundant source of new triploids by crossing with diploids.

(5) Diversification by somatic mutation. Evidence mounts to show that in bananas, as in other vegetatively propagated crops, somatic mutation contributes to variability, though its importance cannot yet be well assessed (Baker & Simmonds, 1951; Simmonds, 1954).

The place of origin of the edible bananas is doubtful. There is reason to think that Malaya was an important centre of origin of the edible diploid forms of *M. acuminata* (Simmonds, 1953*a*). Subsequent hybridization with *M. balbisiana* and the origin of triploidy may well have taken place independently in several different places far removed from each other. Thus hybrid II (AAB) and hybrid III (ABB) bananas are apparently particularly important in peninsular India where *M. balbisiana* is native but *M. acuminata* is unrecorded; this suggests that edible diploid forms of *M. acuminata* and perhaps hybrid diploid types were carried into India from the Malayan region and there hybridized with *M. balbisiana* to produce edible triploids. Conversely, triploid *acuminatas* could hardly have originated in India except from selfing or intercrossing of fertile edible diploids. The most plausible hypothesis as to a centre of origin of the group is therefore Indo-Malaya in general with, perhaps, Malaya as a primary centre and India a secondary one.

Taxonomy. The two Linnaean species, *M. paradisiaca* and *M. sapientum*, can both be identified with reasonable certainty with edible banana clones; the first is the Plantain, the second is Silk Fig (Cheesman, 1948, and in Dodds & Simmonds, 1948*b*). Cheesman treated the Plantain as an edible triploid form of *M. acuminata* and Silk Fig as a hybrid triploid type. The results given in this paper show that both are of hybrid origin and the way is therefore clear for complete rejection of the Linnaean epithets from the taxonomic literature of the wild bananas.

V. SUMMARY

A taxonomic scoring method is used to classify the edible bananas and to provide evidence on their evolution. Edible diploid forms of *Musa acuminata* are thought to be the primary source of the whole group to which another species, *M. balbisiana*, has contributed by hybridization. Thus there exist diploid and triploid edible forms of *M. acuminata* and diploid, triploid and tetraploid hybrid types of genetic constitutions that vary according to their histories. There is a faint possibility that a third wild species has contributed to the origins of a small group of triploid hybrid types. Triploidy was probably established under human selection for vigour and fruit size; tetraploidy is inexplicably rare. The centre of origin of the group is Indo-Malaya and Malaya is probably the primary centre. The two Linnaean species *M. paradisiaca* and *M. sapientum* refer to identifiable edible varieties which are both shown here to be of hybrid origin. The names therefore may be rejected from the nomenclature of the wild bananas.

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APPENDIX 1

Taxonomic scorings of diploids

Material	Stem colour	Petiole form	Ped-uncle	Pedicels	Ovule rows	Bract shoulder	Bract curling	Bract shape	Bract apex	Bract colour	Colour fading	Bract scars	Tepal corru-gation	Male flower colour	Stigma colour	Totals	Notes
Seeded																	
M. acuminata—AA	1·4	1·6	1·9	1·9	1·1	1·4	1·0	1·2	1·3	1·0	1·7	1·2	1·6	1·1	1·6	21·0	*
M. balbisiana—BB	4·7	4·6	5·0	4·7	5·0	4·2	5·0	4·5	4·7	5·0	4·1	4·9	4·1	3·9	4·3	68·7	*
F_1 hybrids—*AB*	2·6	3·4	4·5	3·6	1·6	3·1	2·2	1·9	2·8	3·9	5·0	3·0	1·7	3·6	3·0	45·9	*
Musa sp. (Assam)—*RR*	3·0	1·0	5·0	3·7	1·0	3·0	1·0	1·0	2·3	1·0	1·0	3·0	1·4	1·0	3·7	32·1	*
Edible																	
M. acuminata—AA																	
Sucrier	1	1	2	3	1	5	1	2	1	1	1	1	1	1	1	23	.
Palembang	1	1	1	1	1	5	1	3	1	1	1	1	1	1	3	23	.
Bande	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	16	.
Pisang Lilan	1	1	1	2	1	3	1	1	1	1	1	1	2·5	1	1	19·5	.
Tongat	2	1	1	1	1	3	1	1	1	1	1	2	1	1	3	21	.
Sikuzani	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	16	.
Paka	1·5	1	2	2	1	1	1	1	2	1	(1)	1	1	1	1	18·5	†
Mjenga Maua	1	1	1	3	(1)	1	(1)	1	1	1	1	1	1	1	1	17	‡
'Small Type'	2	1	1	1	1	5	1	1	1	1	1	1	1	1	3	22	.
Means	1·4	1·0	1·2	1·7	1·0	2·9	1·0	1·3	1·1	1·0	1·0	1·1	1·2	1·0	1·7	19·6	.
Hybrid I—*AB*																	
Ney Poovan	3·5	4	4	5	1	4	3	4	3	3	5	2	1	5	1	48·5	.

* Means of 20, 16, 11 and 3 clones respectively.

† A variety with yellow bracts. An arbitrary score is assigned for colour fading.

‡ A variety with persistent bracts. (See text-notes on key characters.) An arbitrary score has been given for bract curling and for ovule arrangement.

APPENDIX 2

Taxonomic scorings of triploids

Material	Stem colour	Petiole form	Ped-uncle	Pedicels	Ovule rows	Bract shoul-der	Bract curl-ing	Bract shape	Bract apex	Bract colour	Colour fading	Bract scars	Tepal corru-gation	Male flower colour	Stigma colour	Totals	Notes
M. acuminata—AAA																	
Gros Michel	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	17	.
Masak Hijau	1	1	1	2	1	1	1	2	1	1	1	1	1	1	2	18	.
Green Red	1	1	1	2	1	1	1	4	1	1	1	1	1	1	3	21	.
'Orotava'	2	1	1	1	1	2	1	2	1	1	1	1	1	1	1	18	.
'Rio'	1	1	1	1	1	3	1	2	1	1	1	1	1	1	1	18	.
Maruthuva	1	1	4	1	1	3	1	2	1	1	1	1	1	1	1	21	.
Rajah	2	2	1	3	1	1	1	1	2	1	1	1	1	1	1	20	.
Palimbang	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	16	.
Gitigi	1	1	1	3	1	1	1	1	1	1	1	1	2	1	1	18	.
Mutika	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15	.
Lujugira	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	16	.
Nambi	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15	.
Kitarasa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15	.
Lwekilo	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	16	.
Ntobe	1	1	1	1	1·5	1	1	4	1	1	1	1	1	1	1	18·5	.
Means	1·1	1·1	1·2	1·5	1·0	1·4	1·0	1·7	1·1	1·0	1·0	1·0	1·1	1·0	1·3	17·5	.
Hybrid II (1)—natural																	
Mysore	2	2	1	5	1	4	1	3	3	3	5	3	1	4	3	41	.
King	2	2·5	1	3	2	1	1	2	1	5	5	3	1	1	3	33·5	*
Celat	2	3·5	1	3	3	4	2	1	1	3	5	1	1	3	3	36·5	*
Pome	3	2	4	4	2	5	1·5	5	2	3	4	2	1	4	3	45·5	.
Nadan	3	2	2	4	1	3	1·5	4	1	3	3·5	2	1	2·5	3	36·5	.
N. Padaththi	3	1	2	4	1	2	2·5	4	2	3	3	2	1	5	3	38·5	.
Silk	2	3	1	2	1	1	1	1	1	3	5	1	1	2	1	26	.
Means	2·4	2·3	1·7	3·6	1·6	2·9	1·5	2·9	1·6	3·3	4·4	2·0	1·0	3·1	2·7	36·7	.

Hybrid II (2)—natural																
Horn Plantain	2·5	3·5	2	5	2	(3)	4	1	1	3	5	3	1	1·5	3	40·5	†, ‡
French Plantain	(3)	3	3	4	3	3	(3)	3	1	3	5	3	1	2	2	42	†, §
Grindy	3	2·5	1	3	3	3	3	5	1	2	3	2	1	2·5	3	38·0	†
Sept-semaines	4	3	5	3	1	4	2	3	3	4	5	4	1	1	3	46	†
Means	3·1	3·0	2·7	3·7	2·2	3·2	3·0	3·0	1·5	3·0	4·5	3·0	1·0	1·7	2·7	41·6	.
Hybrid II (1) experimental																
3302 B	2	3	1	2	4	1	2·5	3	2	4	4	2	1	2·5	1	35	‖
3530	3	2	4	1	1	3	2	1	1	2	3	1	1	1	5	31	‖
3606 C	3	2	2	4	(2·5)	1	3	2	1	3	5	2	1	1	1	33·5	‖
Means	2·7	2·3	2·3	2·3	2·5	1·7	2·5	2·0	1·3	3·0	4·0	1·7	1·0	1·5	2·3	33·2	.
Hybrid III—natural																
Bluggoe	4·5	4·5	5	5	5	5	2·5	5	2	5	5	3	1	5	5	62·5	.
Awak Legor	4	5	5	5	5	5	3·5	3	3	4	5	3	1	5	3	59·5	.
Peyan	4·5	5	3	4	4	5	4	3	3	5	5	3	1	5	5	59·5	.
Ney Mannan	4	4	5	5	5	3	2	5	4	5	5	1	1	5	5	59	.
P.B. Bathees	5	5	5	5	5	5	3·5	4	1	5	5	2	1	5	5	61·5	.
Means	4·4	4·7	4·6	4·8	4·8	4·6	3·1	4·0	2·6	4·8	5·0	2·4	1·0	5·0	4·6	60·4	.
Hybrid III—experimental																
3302 A	3·5	3·5	5	5	5	1	5	5	3	5	5	3	1	4	3	57·0	‖
3484—1	4	5	5	5	5	4	4	4	3	5	4	3	1	3	5	60	‖
3484—3	4	5	5	5	5	3	4	4	3	4	5	3	1	4	5	60	‖
Means	3·8	4·5	5·0	5·0	5·0	2·7	4·3	4·3	3·0	4·7	4·7	3·0	1·0	3·7	4·3	59·0	.

* Incorrect origins assigned to these varieties by Dodds & Simmonds (1948*b*).

† The varieties of this small group are distinctive in having yellow flowers, a character not seen in either *M. acuminata* or *M. balbisiana* (see text).

‡ The male bud of the Horn Plantain is small and rapidly deciduous. An arbitrary score has been given for bract shoulder.

§ A variety with persistent bracts; an arbitrary score has been given for bract curling. At least one somatic mutant has heavy black stem markings.

‖ 3302 A and 3302 B are triploid backcross progeny of an F_1 hybrid; the other experimental seedlings are from crosses of tetraploids (*AABB*), I.C. 57 and I.C. 61, with the wild species. Ovule arrangement in 3606 C unknown; arbitrary score inserted.

APPENDIX 3

Taxonomic scorings of tetraploids

Material	Stem colour	Petiole form	Ped-uncle	Pedicels	Ovule rows	Bract shoul-der	Bract curl-ing	Bract shape	Bract apex	Bract colour	Colour fading	Bract scars	Tepal corru-gation	Male flower colour	Stigma colour	Totals	Notes
M. acuminata—experimental																	
I.C. 1—Gros M. × *AA*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15	.
I.C. 2—Gros M. × *AA*	1	1	1	1	1	1	1	1	1	1	3·5	1	1	1	1	17·5	.
I.C. 43—Rajah × *AA*	3	3	1	2	1	1	1	1	1	1	1	1	1	1	1	20	.
Means	1·7	1·7	1·0	1·3	1·0	1·0	1·0	1·0	1·0	1·0	1·8	1·0	1·0	1·0	1·0	17·5	.
Hybrid IV—experimental																	
I.C. 21—Mysore × *AA*	1	3	1	3	(1)	5	1	1	1	3	2	1	1	1	2	27	*
I.C. 22—Mysore × *AA*	1	2	1	4	1	3	1	3	3	3	5	3	1	1	3	35	.
I.C. 25—Mysore × *AA*	1	2·5	1	2	(1)	3	1	1	1	3	5	3	1	1	1	27·5	*
I.C. 31—Pome × *AA*	2	2·5	3	3	3	1	1	1	1	3	5	2	1	2	1	31·5	.
I.C. 62—Pome × *AA*	2·5	1	1	3	1	1	1	2	2	3	5	1	1	3	1	28·5	.
Means	1·5	2·2	1·4	3·0	1·4	2·6	1·0	1·6	1·6	3·0	4·4	2·0	1·0	1·6	1·6	29·9	.
Hybrid V—experimental																	
I.C. 24—Mysore × *BB*	3	3	4	5	2·5	3	1	3	3	3	5	3	1	5	3	47·5	.
I.C. 57—Awak L. × *AA*	3·5	4	5	5	3	5	1·5	3	1	4	5	1	1	2	2	46·0	.
I.C. 61—Awak L. × *AA*	3·5	5	5	5	2	2	2	3	3	4	5	1	1	2	1	44·5	.
Means	3·3	4·0	4·7	5·0	2·5	3·3	1·5	3·0	2·3	3·7	5·0	1·7	1·0	3·0	2·0	46·0	.
Hybrid VI—natural																	
Tiparot	4	5	5	5	5	5	5	5	5	5	5	4	1	3	5	67	.
Hybrid VI—experimental																	
I.C. 36—Bluggoe × *BB*	5	5	5	5	5	5	3	3	3	5	5	5	1	5	3	63	.
I.C. 55—Awak L. × *BB*	5	5	5	5	5	5	4	5	4	5	5	2	1	5	5	66	.
Means	5·0	5·0	5·0	5·0	5·0	5·0	3·5	4·0	3·5	5·0	5·0	3·5	1·0	5·0	4·0	64·5	.

* Ovule arrangement unknown; arbitrary scores inserted.

Some features in the morphology of a hitherto undescribed stem from the Lancashire Coal-measures. By H. S. Holden.

(With Plate **22** and 8 Text-figures)

[Read 4 November 1954]

The stem which is the subject of this paper was found in a coal ball from the Lancashire Coal-measures collected at Shore near Littleborough. It is represented by two transverse sections only, both of which occur in the same slide, and although efforts have been made to locate the petrified block from which the slide was cut these have, unfortunately, proved unsuccessful.

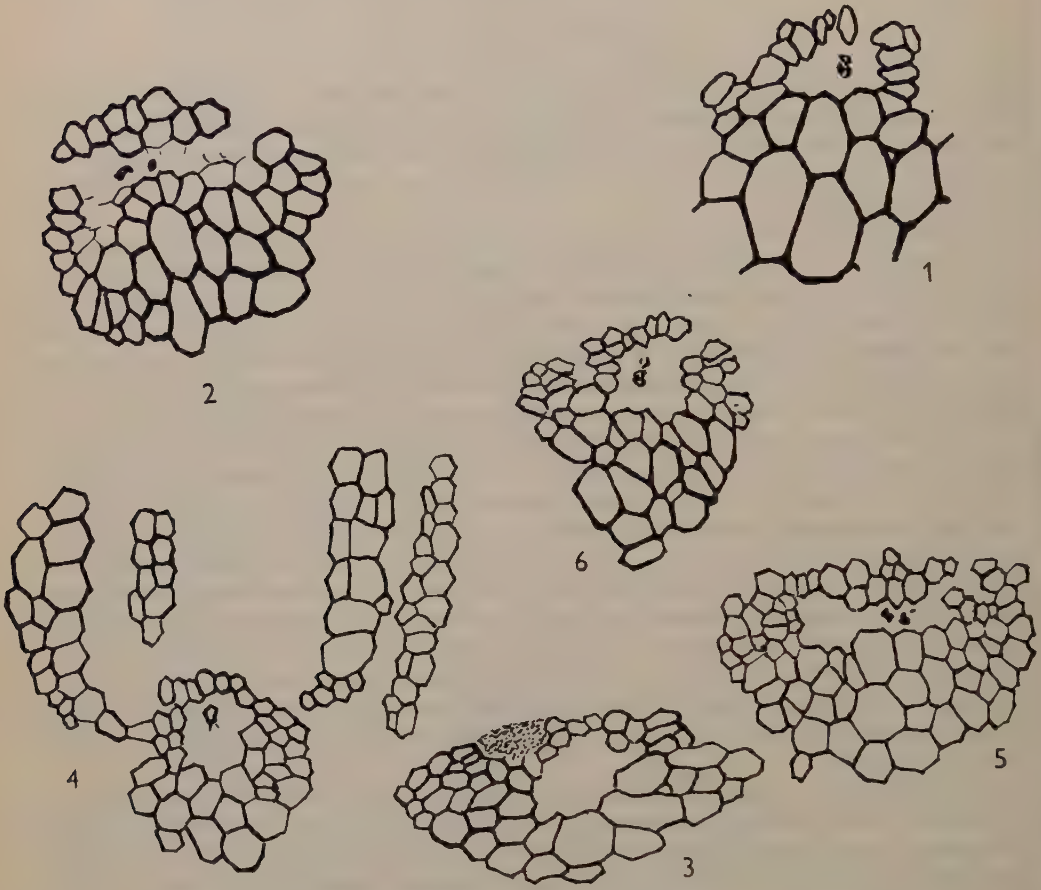
The larger of the two sections is in some respects the better preserved, the smaller one having suffered some damage and tissue alteration before becoming petrified. Both sections possess a pronouncedly stellate outline with five arms. It seems clear that the stellate outline is due to the decurrent bases of the petioles, a feature in which they recall the stem sections of *Heterangium* (Scott, 1923). The individual arms of the star are unequal in size, and one of the more prominent ones in the larger stem contains a single comparatively large leaf trace, a feature shown by none of the others (Pl. **22**, figs. 1, 2).

The stelar xylem consists entirely of primary tracheids in the form of an almost solid cylinder and no indications of cambium have been detected. Its diameter in the larger stem is approximately 0·8 mm. and in the smaller 0·35 mm. The pitting of the metaxylem tracheids is multiseriate and is not confined to the radial walls (Pl. **22**, fig. 3). The protoxylem is mesarch and consists of a number of discrete groups of small tracheids distributed round the periphery of the stele. Each group is partly or wholly enclosed in a small pocket of parenchyma surrounding which is a sheath of metaxylem, the constituent tracheids of which are of smaller calibre than those forming the inner part of the stele (Text-fig. 1; Pl. **22**, fig. 2). The outer members of each of these groups of smaller tracheids are clearly centrifugal in origin. There is a minute non-vascular core the tissues of which are not preserved in the larger stem, but in the smaller one they appear to be wholly parenchymatous.

In the latter the recognizable protoxylem groups are five in number and are spaced at regular intervals round the periphery of the stele (Pl. **22**, fig. 4). Here they form small projecting masses which give the transverse section of the stem a polygonal outline. The metaxylem is clearly divided into three equal segments separated from one another by three symmetrically placed parenchymatous rays which unite in the centre of the stem and extend to the outer margin of the stele (Pl. **22**, fig. 4). This stem also shows traces of the phloem on three faces of the xylem pentagon. There are indications in the larger stem of three similar symmetrically situated radial breaks in the continuity of the otherwise homogeneous metaxylem cylinder, one of these being opposite the outgoing leaf-trace (Pl. **22**, fig. 2); and the two others being indicated at ‘B’ and ‘C’ in the same figure.

The leaf-trace present in the larger stem, to which reference has already been made, consists of a central group of protoxylem enclosed in parenchyma which in turn is surrounded by metaxylem (Text-fig. 2). The metaxylem tracheids forming the abaxial part of the leaf-trace are much fewer in number and are of smaller calibre than those forming the adaxial part, and the appearance of the leaf-trace as a whole suggests that it has been formed by the detaching of one of the peripheral protoxylem groups and its associated group of small metaxylem tracheids from the parent stele. This is borne out by the fact that, opposite the point of departure of the leaf-trace, there is a gap in the continuity of the more superficial tracheids of the stem stele. This gap is more or less V-shaped in transverse section, but the tracheids on its outer margins curve inwards towards each other suggesting that the gap is in the process of closure (Text-fig. 7).

The cortex, in both stems, shows a well-marked division into two zones, the outer one of which consists of from three to five rows of comparatively small parenchymatous cells with firm walls and apparently without intercellular spaces. This outer zone is pale brown in colour and at first sight looks sclerenchymatous but this appearance is deceptive and is due to the cell contents, which, in many of the cells, have shrunk away from the cell-walls in the form of a thick well-defined ring (Text-fig. 8). The cells of the inner zone are larger and thinner-walled and form a looser tissue with intercellular spaces between the constituent cells. This looser tissue appears to interrupt the continuity of the outer cortical zone on either flank of the stellate arms and extends, in these areas, to the



Text-figs. 1–6. (All figs. × 75).

Text-fig. 1. One of the peripheral mesarch protoxylem groups of the new stem.

Text-fig. 2. Transverse section of the xylem of the leaf trace.

Text-fig. 3. Transverse section of the xylem of the leaf trace of *Heterangium grievii* from Slide 1293. Williamson Collection.

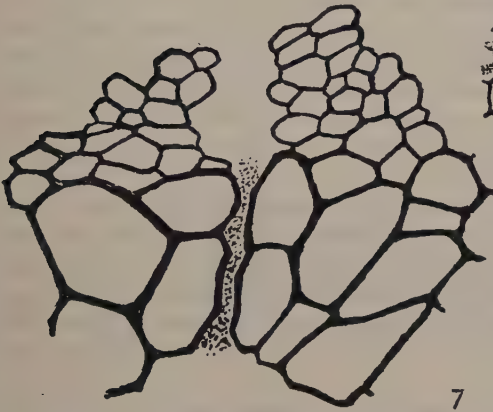
Text-fig. 4. Transverse section of the xylem of the leaf trace of *Lyginopteris heterangioides* at a stage in which it is still enclosed in the stem stele showing the secondary xylem associated with it at that stage (Scott Coll. no. 3457).

Text-fig. 5. Transverse section of the xylem of the leaf trace of *L. heterangioides* lying in the stem cortex (Scott Coll. no. 3457).

Text-fig. 6. Transverse section of the xylem of one of the twin leaf trace bundles of *Lyginopteris oldhamia* (Williamson Coll. no. 1884).

epidermis. It is not unlike the pneumathode tissue found in the petioles of *Pteridium aquilinum* and other ferns (Bower, 1923, p. 169) and may have had a similar function. The cortex is bounded externally by a small-celled epidermis which is smooth and devoid of hairs.

Consideration of the anatomical features of the two stems described above points strongly to their belonging to some pteridosperm genus. The relatively large mesarch leaf-trace with its preponderance of centripetal wood, the monostelic stem structure, the mesarch, peripherally situated protoxylem groups and the multiseriate pitting of the metaxylem tracheids are all features which are characteristic of many of the genera of this alliance. We at once encounter difficulties however when we attempt to assign it to any of the genera of which the anatomy is known.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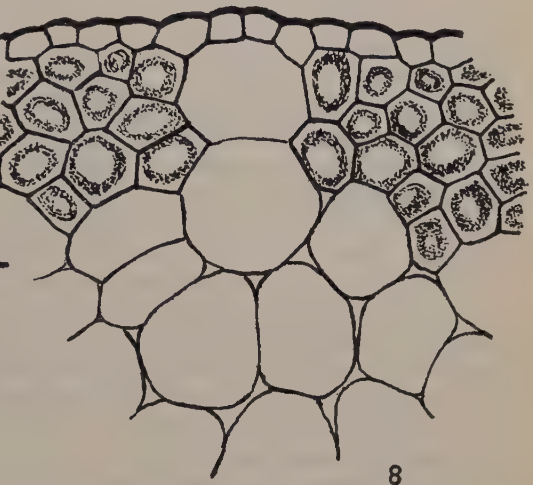
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Text-fig. 7. Portion of the xylem of the larger stem showing the gap in the peripheral tracheids and traces of the radial separation of the metaxylem. (× 200.)

Text-fig. 8. Portion of the cortex of the larger stem showing the division into inner and outer zones. (× 200.)

If we confine ourselves to a consideration of the leaf-trace we find there is a striking similarity between that of our plant and that of those members of the Lyginodendreae possessing a monodesmic mesarch leaf-trace. Scott (1917, 1923) has grouped together all the species of *Heterangium* possessing such a leaf-trace in the subgenus *Eu-heterangium*. This subgenus includes *Heterangium grievii* from the Calciferous Sandstones (Lower Carboniferous) and several of the species described by Kubart (1914) from the Upper Carboniferous beds of Ostrau (e.g. *H. alatum*, *H. schusteri* and *H. minimum*). In some of these (e.g. *H. grievii*) the initially single protoxylem group divides into two and the leaf-trace bundle increases in size tangentially as it moves outward into the cortex, whilst in others (e.g. *H. schusteri*, *H. minimum*) the leaf-trace itself divides into two on leaving the stem stele. In a second group of species of *Heterangium*, included by Scott in the subgenus *Polyangium*, the leaf-trace from its inception consists of two separate bundles (e.g. *Heterangium tiliaeoides*, *H. shorense*, *H. lomaxii*), a feature which is shared by that of *Lyginopteris oldhamia*. It is a point of some interest, however, that another species of *Lyginopteris*, *L. heterangioides*, from the Ostrau beds, possesses a single leaf-trace bundle similar in all essentials to that of *Heterangium grievii*. If we compare the leaf-trace bundle of our plant with that of either *H. grievii* or of *Lyginopteris heterangioides* the close resemblance is obvious (Text-figs. 3–5; Pl. 22, figs. 5, 6). The xylem in most of the petrifactions of *Heterangium grievii* suffers from a greater or less amount of distortion and partial collapse, but one section of this plant in the Williamson Collection (no. 1293), though somewhat thick by modern standards, shows a relatively uncrushed leaf-trace just projecting from the stelar xylem into the cortical tissues (Text-fig. 3). There is also a beautifully preserved stem present in slides nos. 1015 and 1016 in the Scott Collection, and in a companion slide of the same stem, no. 512, in the Kidston Collection, in which the structure of the leaf-trace is well-nigh perfect. The stem and leaf-trace in the Kidston slide have already been figured by Gordon (1912, Pl. III, figs, 21, 22), and a leaf-trace from slide no. 1016 is shown in Pl. **22**, fig. 5, of the present paper. The Scott Collection also fortunately includes a slide, no. 3457, of the stem of *Lyginopteris heterangioides* in which it has been possible to study the leaf-trace. The xylem of this trace is shown as seen in transverse section in Text-figs. 4 and 5. Text-fig. 4 shows the trace at an early stage in its outward course, in which it is still intrastelar and in which it is accompanied by a wedge-shaped group of secondary tracheids on its outer face. Text-fig. 5 is a later stage, in which the secondary tracheids have disappeared and in which the leaf-trace has become larger and shows some indication of tangential spread. The relation of this leaf-trace to the outer margin of the secondary xylem is shown in Pl. **22**, fig. 6. It will be evident that *Heterangium grievii*, *Lyginopteris heterangioides* and our plant all agree in possessing an initially monodesmic leaf-trace characterized by a mesarch protoxylem enclosed in a parenchymatous sheath which, in turn, is enclosed by metaxylem tracheids, the majority of which are centripetal and in which the centrifugally developed tracheids are of smaller calibre. This structural agreement is also shown by each of the paired bundles forming the double leaf-trace of *L. oldhamia* (Text-fig. 6) (Williamson & Scott, 1895).

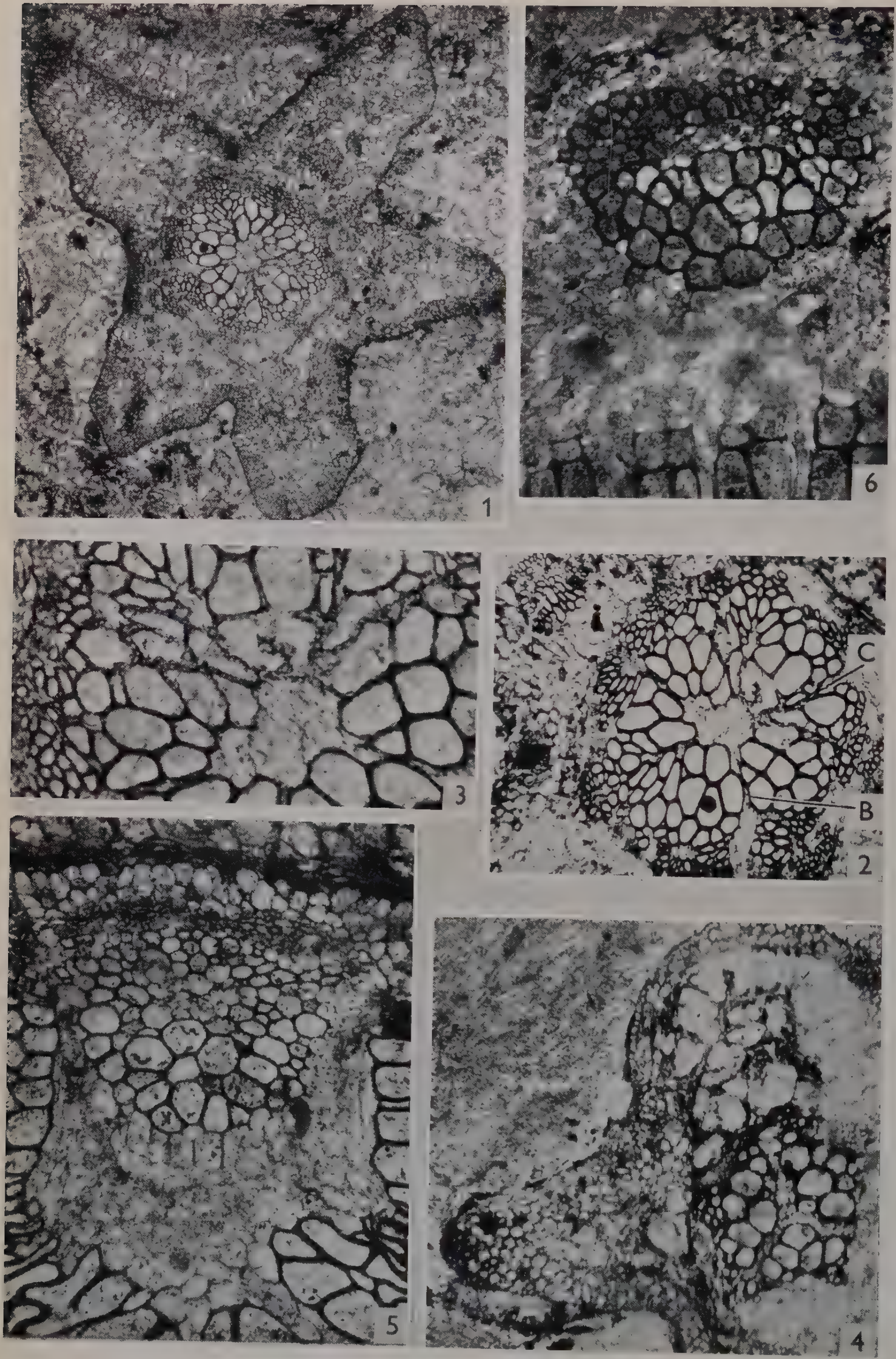
When we come to consider the remaining features of the anatomy of the new stem, however, the differences between it and the Lyginodendreae are too pronounced to render its inclusion in that group logical. Instead of a highly differentiated cortex, in the inner zone of which either groups or horizontal plates of thick-walled stone cells are developed and an outer zone with longitudinally running fibrous bands, or both, we have a relatively simple, wholly parenchymatous condition with some differentiation into inner and outer zones.

The main mass of the stelar xylem is also fundamentally different from that of any of the Lyginodendreae and shows a condition much closer to that of *Stenomyelon tuedianum* (Kidston & Gwynne-Vaughan, 1912). In the stem of this plant the primary metaxylem consists of a three-lobed homogeneous mass of tracheids with no admixture of parenchyma. In transverse section it takes the form of a bluntly triangular mass the lobes of which are more or less separated from one another by narrow strips of parenchyma which meet in the centre of the stem to form the 'narrow pith'. Whilst our plant agrees with *S. tuedianum* in possessing primary metaxylem consisting wholly of tracheids, and in these being divided into three groups by vertical plates of parenchyma, there is no evidence of the pronounced lobing typical of the latter. *Stenomyelon* also differs in the fact that definite protoxylem groups are only developed in the stem in connexion with the emission of the leaf-traces and that each of these is initiated as a pair of exarch groups linked by a large ovoid mass of metaxylem.

It seems clear that, scanty though the available material is, the establishment of a new genus is desirable for the plant described in this paper and the name *Syncrama* (from the *mixture* of characters) is suggested as suitable with the following diagnosis:

Syncrama gen.n.

Stem monostelic with five prominent acute ridges produced by the decurrent leaf bases; cortex devoid of stone cells or longitudinally running fibres, but differentiated into a firm-textured outer zone and a looser textured inner zone; metaxylem consisting of a cylinder of tracheids with multiseriate pitting on all walls, devoid of parenchymatous inclusions, but separated into three groups by narrow rays of parenchyma which unite to form a small non-vascular core in the middle of the stem: protoxylem mesarch in the form of



Sections of *Syncrama liratum* and allied species

(*Facing p.* 317)

discrete peripheral groups: leaf-trace monodesmic, mesarch, with the protoxylem enclosed in a parenchymatous sheath surrounded by tracheids which are of smaller calibre than those of the axis metaxylem: centripetally developed tracheids of the leaf-trace much more numerous and larger than those developed centrifugally.

S. liratum sp.n. Type and only species with diagnosis as for the genus.

The slide containing the type sections has been presented to the Geological Department, British Museum (Natural History), and the number V. 31899 has been assigned to it.

Acknowledgements

Grateful acknowledgements are due to Mr W. N. Edwards, Keeper of the Geological Department (British Museum), not only for facilities for studying the relevant material in the Williamson and Scott Collections, but also for his help with regard to the choice of suitable generic and specific names for the plant stem described in this paper. I am also much indebted to my former colleague, Mr G. Salter, for the negatives and prints from which Pl. **22**, figs. 2, 4 and 5, were made, and to the Photographic Department of the British Museum with regard to Pl. **22**, fig. 6. Acknowledgements are also due to the Royal Society for the loan of a microscope in connexion with this investigation.

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EXPLANATION OF PLATE 22

Fig. 1. Transverse section of the larger stem showing the stele, cortex and stellate outline. (× 25.)

Fig. 2. Stele of the same stem to show detail. Note the leaf-trace at the upper left-hand corner of the figure and the traces of the three gaps in the metaxylem. (× 50.)

Fig. 3. A portion of the stele more highly magnified. The multiseriate pitting of the tracheids can be seen in the upper part of the figure. (× 200.)

Fig. 4. Transverse section of part of the smaller stem. (× 60.)

Fig. 5. Transverse section of the leaf-trace of *Heterangium grievii*, Scott Coll. no. 1016. (× 90.)

Fig. 6. Transverse section of the leaf-trace of *Lyginopteris heterangioides*, Scott Coll. no. 3457. (× 90.)

Notes on Cameroons Commelinas, Commelina cameroonensis sp.nov. and C. mannii C. B. Clarke redescribed.

By J. K. MORTON, Ph.D. University College of the Gold Coast. (Communicated by Dr George Taylor, Sec.L.S.)

(With 1 Text-figure)

[Read 21 April 1955]

Commelina cameroonensis J. K. Morton, sp.nov.

Herba magna et vaga, *C. capitatae* Benth. similis; caulis ascendens et per virgulta silvarum palans, ex nodis inferioribus radicans, praeter lineam capillorum in internodiis superioribus glaber. *Foliorum* vagina longa (usque ad 2·5 cm.), circum apicem et ad margines conjunctos longe rubro-ciliata, alibi fere glabra; lamina ovato-lanceolata, basi valde inaequilatera et in petiolum brevem rotundata, apice longe acuminata, plerumque ter vel quater longior quam lata (5·5–11·5 × 1·7–3 cm.), supra glabra, infra ad nervos principes ciliata. *Spathae* in foliorum superiorum axillis sessiles, 1–3-natae, marginibus conjunctis, breves (quadrante longiores quam latae), apice lato acutae nec acuminatae, mucilaginem continentes. *Flores* magni (*c.* 2 cm. diam.), e spatha paullum eminentes, mane expandentes, ante meridiem clausi. *Sepala* obtusa, concava, glabra. *Petala* alba, 2 superiora longe unguiculata, inferius bene formatum cordatum sepalis majus. *Stamina* fertilia 3, antheris luteis; staminodiorum 3 antherae infertiles magnae (1·25 mm. longae), pallide luteae, lobis 2 basalibus magnis extrorsus curvatis, lobis 2 apicalibus minoribus, lobis 2 intermediis vix obviis. *Capsula* magna (7 mm. longa et lata), vix crassa, loculis 2, 1-spermis; semina laevia, fusca, 3·75 × 2·25 mm.

Habitat in silvis humidis inter 1200 et 2500 m. alt. in Monte Cameroonensi (Morton G. C. 7116), Fernando Po (Herb. Inst. Fr. Af. Nr. 10423) et in collibus Bamendae (F.H.I. 28475).

Typus. J. K. Morton G.C. 7116 ex Monte Cameroonensi, mense Aprili 1952, in Herb. Gold Coast. Isotypi in Herb. Brit. Mus. et Herb. Kew.

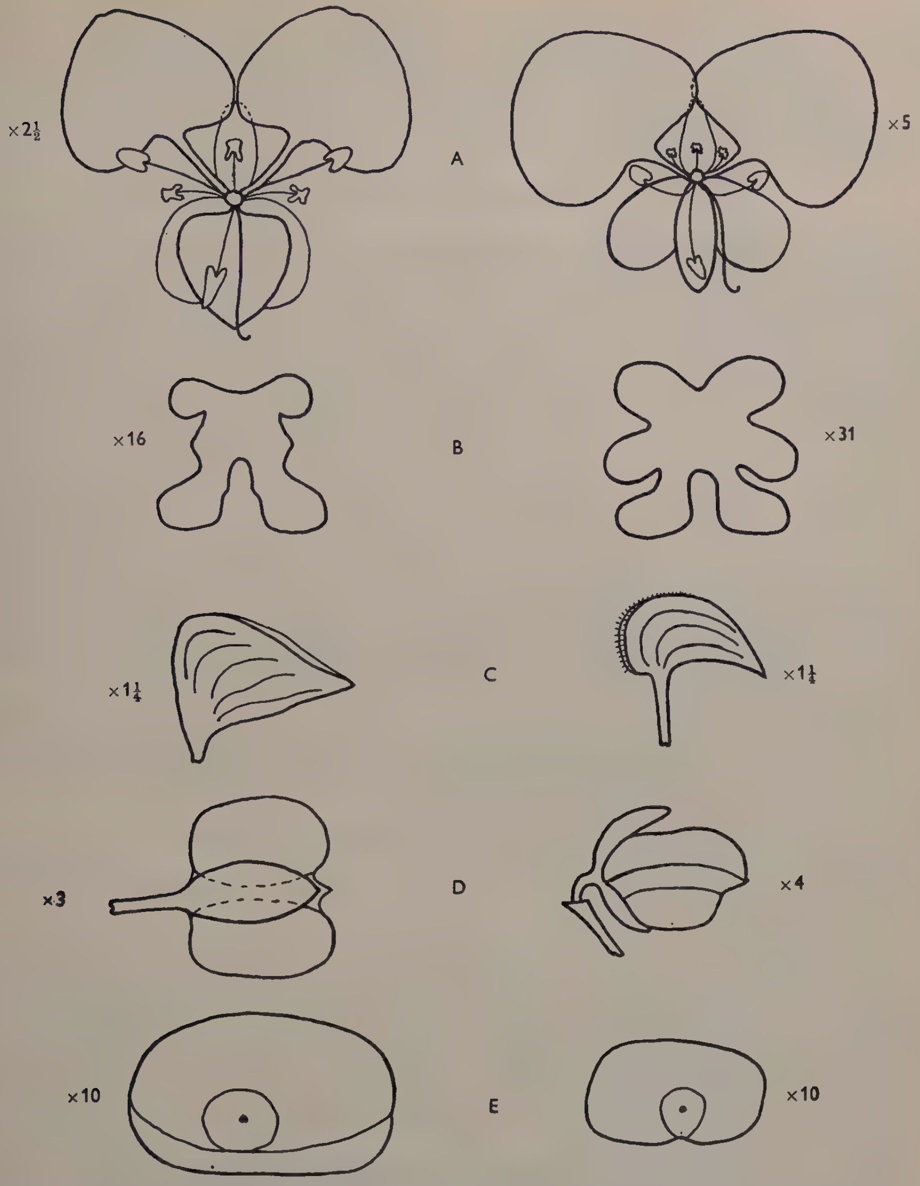
A very distinct plant, resembling *C. capitata* in general appearance, but differing in its pure white flowers, smaller number of spathes, and in capsule and seed characters.

Commelina mannii C. B. Clarke

C. B. Clarke in A. & C. DC., *Monogr. Phan.* **3**, 167 (1881); Hutch. in Hutch. & Dalziel, *Fl. W. Trop. Afr.* **2**, 317, 318 (1936).

A redescription of this species, based on material collected by the writer in the type-locality, is considered to be desirable in view of the inadequacy of Clarke's original description and the misleading interpretation of this in the *Flora of West Tropical Africa*.

A *small creeping herb* resembling *C. diffusa* Burm. f.; stem with medium internodes, glabrous save for a line of hairs on the upper internodes, rooting from the lower nodes. *Leaves* small; sheath loose, usually suffused with a purplish colour, glabrous save for a few short colourless cilia around the top and along the fused margins; lamina thick, ovate, closely sessile on the sheath and clasping the stem, broadly acute to obtuse (not acuminate at the apex), usually about 2 cm. long and 1·4 cm. broad but sometimes longer, finely ciliate on the margins. *Spathes* borne singly in the axils of the upper leaves, small (averaging 13 × 6 mm.), with free margins and recurved keel, glabrous or nearly so except for short cilia on the margins, containing some mucilage at the time of flowering; peduncles as long as the spathe, spreading or recurved. *Flowers* small (9 mm. in diam.), very shortly exserted, opening early in the morning. *Sepals* obtuse and concave, glabrous. *Petals* orange-yellow, the 2 upper with a very short claw, the lower one small and subulate. *Anthers* 3, orange, on short filaments; infertile anthers of staminodes 3, yellow, small (0·7 mm. long), with three pairs of almost equal spreading lobes. *Capsule* small (5 × 3·5 mm.) 2 to 3-locular; lower loculus indehiscent; upper loculus or loculi



Commelina cameroonensis sp.nov. *Commelina mannii* C. B. Clarke

Fig. 1. A, Face view of flowers; B, infertile anthers of staminodes; C, spathes; D, fruits (side view of *C. cameroonensis*, top view of *C. mannii*), E, seeds.

dehiscent with 2 (rarely 1) seeds per loculus; seeds small (2·5 × 1·4 mm.), obscurely wrinkled and very finely reticulate, dark brown.

HABITAT. In rich damp soil in sunny clearings in the mist-forest and in sheltered places in the grassland above. From 2000 to 3000 m. altitude on Cameroons Mt. Widely distributed in the mountainous regions of tropical Africa.

EXSICC. Mann 2136 (Type in Herb. Kew) from Cameroons Mt., J. K. Morton G.C. 7093 (K., B.M., G.C.) from Mann's Spring, Cameroons Mt.

The writer's thanks are due to Mr Dandy for assistance in preparing the manuscript.

The Dick Herbarium. By SIR GAVIN DE BEER, F.R.S., F.L.S.

(With Plate **23**)

[Read 24 May 1955]

In the *Biographical Index of British and Irish Botanists* by J. Britten and G. S. Boulger, third Supplement (London, 1908), p. 4, there is to be found the name of 'James Dick', described as a 'pupil of Haller'. As a matter of fact, Johann Jacob Dick was neither British nor Irish, but Swiss, and his name was placed in parentheses in subsequent editions of the *Index*. The reasons for his inclusion have never been given, but an explanation of this mistake will be found at the end of this paper. Meanwhile, it may be of interest to reconstruct what is known of the life and work of Dick, for they are material to the curious set of circumstances which at one time led to the belief that he was British.

Johann Jacob Dick was born in 1742 at Berne of a family[1] which, since the sixteenth century, had provided five members of the Great Council and nineteen clerks in holy orders. In 1758 Albrecht von Haller[2] was appointed to the post of director of the salt works at Bex and lived in the neighbouring village of Roche, where he attached Dick to his household as a pupil and tutor to his children. A sidelight on Haller's household and Dick is provided from an unexpected quarter, namely the *Mémoires*[3] of Casanova. This adventurer was travelling through Switzerland in 1760 and went to stay with Haller at Roche. The relevant passage of his *Mémoires* reads as follows (translated):

> He [Haller] had a charming daughter of about 18 years of age and modest demeanour who only opened her mouth at table to speak occasionally in a low voice to a young man sitting beside her. After dinner, finding myself alone with M. Haller, I asked him who was this young man. He replied that he was his daughter's tutor.
>
> Such a tutor and so pretty a pupil might easily become two lovers.
>
> Please God.
>
> This Socratic reply made me see how very much out of place my remark had been, and I felt ashamed of myself.

The period during which Dick was living at Roche was that when Haller was collecting materials for his great work on the Swiss flora, the *Historia Stirpium indigenarum Helvetiae inchoata*, which was eventually published at Berne in 1768. For this purpose Haller sent out in all directions his friends, pupils and the members of his staff of foresters. Dick took part in these forays and was mentioned in the preface to Haller's book: 'The Rev. Mr Dick visited the Valaisan Alps of Salanfe, Herbagère, Combe de Martigny, and Valorsine'.

From the *Emendationes* which Haller published, it appears that it was in 1762 that Dick undertook these journeys. His colleagues included the Rev. Abraham-Louis de Coppet,[4] Bernard-Jean-François Ricou,[5] the surgeon of Bex, and the celebrated Pierre Thomas[6] and his son Abraham Thomas,[7] who were among the most skilled and experienced finders of plants in Central Europe.

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[1] Carl Wilhelm Dick: 'Further genealogical notes on the Dick family of Bern and Kassel', *Genealogists' Magazine*, **11**, 1953, p. 849.

[2] Albrecht von Haller, 1708–77, F.R.S., of Berne.

[3] *Mémoires de Jacques Casanova de Seingalt.* Edition Garnier, Paris, **4**, 1910, p. 422.

[4] Abraham-Louis de Coppet, 1706–85.

[5] Bernard-Jean-François Ricou, 1730–98, surgeon, of Bex.

[6] Pierre Thomas, 1708–81, forest-warden, of Bex.

[7] Abraham Thomas, 1740–1824, son of Pierre, forest-warden and naturalist of Bex. On the Thomas family see: F. Cosandey: 'Les naturalistes Thomas et leurs amis.' *Revue Historique Vaudoise*, **50**, 1942, p. 81.

While Haller's team operated from Roche to supply him with valuable information about the flora of the south-western Alps, he was very anxious to obtain specimens from the south-east, and particularly from the Grisons and the Valtelline which in those days belonged to that republic. To his great friend Johann Gesner[1] of Zürich, Haller wrote on 22 April 1763, '. . . I expect to send my sons' tutor to the Valtelline, and I set high hopes on that region which produces olives. . . .'[2]

A month later Haller wrote again to his friend Gesner:

> Roche, 24 May, 1763. . . . This letter will be handed to you by Dick, my sons' tutor, a student of theology, who is animated by an ardent love of botany. I am sending him at my own expense to Chiavenna and the Valtelline, with high hopes of what he will be able to find during the three weeks that he will be there. I beg you from our friendship to see that he has letters of recommendation for the Grisons, where it is not always possible to live safely and to make excursions. It would be of great advantage if some merchant were to recommend him to his colleagues at Chiavenna, Morbegno, Teglio or Tirano. . . .[3]

Gesner replied as follows on 8 June 1763:

> 'The gentle Dick had brought me your very welcome letter. I recognize in him an expert and indefatigable botanist, very well versed in the flora of Switzerland. You and all botanists will derive great advantage from his journey. I have been delighted to use what good offices I could, and have given him a letter of introduction to Coire. Füssli,[4] a young man of great promise, son of the painter, has joined the party. For some time he has addressed himself to the study of medicine, and, devoted to his work and very curious to penetrate the secrets of nature, he has acquired a profound knowledge of insects. A young nobleman, von Meis,[5] an intimate friend of Füssli's, has also joined the party, and by this means the three will be able to help one another. Dick has been suffering from a swollen eye which has caused him some pain. He has tried scarification without however benefiting much from this remedy. Nevertheless, he has insisted on setting out so as not to delay the undertaking.[6]

Meanwhile, Dick himself wrote[7] to Haller to say that he stayed longer in Zürich than he had expected, partly because of the heavy rains and the assurance he had received from Gesner and many others that the mountains would still be covered with snow, and partly in the hope of obtaining some companions on his journey. He went on to say that if he had not feared that during their stay Thomas would waste too much money, he would have waited even longer for warmer and better weather. He had left Zürich on the previous Monday [June 6] in the afternoon with two young gentlemen from Zürich, Junker von Meis, and Mr Füssli who had devoted himself to natural history for some time and was particularly skilled in his knowledge of insects, and was also something of a draftsman. Both were recommended by Mr Gesner. They had arrived at Coire without mishap although wet through to the skin. Mr Gesner, Director Schulthess and Mr Haller had given him letters of recommendation to Coire and Chiavenna. Most of these had resulted in further letters so that he had every hope of completing the journey profitably.

Everybody in Coire told him that the Albula and Septimer passes were still so deeply covered with snow that few plants would be found there, and he hoped that Haller would not object if he travelled over the Splügen Pass to Chiavenna and from there went up the Valtelline, over the Bernina Pass and if possible over the Albula, Julier and Septimer Passes again to Chiavenna, and from there back to the Valais. During the time he was searching in the Valtelline, the snow would be reduced on the mountains and give greater hopes of finding fine plants.

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[1] Johann Gesner, 1709–90, of Zürich.

[2] G. R. de Beer: 'Haller's Historia Stirpium', *Annals of Science*, 9, 1953, p. 38, letter 132.

[3] *Ibid.* letter 133.

[4] Johann Caspar Fuessli, 1745–86, of Zürich, third son of the painter Johann Caspar Fuessli; brother of John Henry Fuseli, 1741–1825). He was the author of *Verzeichniss der ihm bekannten schweizerischen Insecten*, Zürich 1775, and several other works.

[5] Hans Ludwig von Meiss, 1745–95, councillor of Zürich.

[6] *Epistolarum ab Eruditis Viris ad Alb. Hallerum scriptarum* Pars I, Bernae, 5, 1774, p. 141, letter 195. Gesner to Haller.

[7] Bürgerbibliothek Bern: Hallersche Briefsammlung, 1763, O.D.

The itinerary of the party was succinctly described by Haller in his *Historia Stirpium*:[1]

> The Rev. Mr Dick in company with the forest warder Abraham Thomas made a journey at my expense through Coire, the Splügen Pass, Chiavenna, the Valtelline, the Umbrail Pass, the mountains of Trone and Fräela, the Bernina Pass, and the very high Septimer Pass. Thence by way of the Furcula, Mesocco, Bellinzona, the Gries Pass and the Valais, he returned to Roche, laden with many rare plants.

In filling out the details of the itinerary, some mistakes were made by Heinrich Dübi[2] who contended that from the Septimer Pass, Dick and his friends crossed the Forcellina Pass to Avers and reached Bellinzona by way of San Bernardino Pass. That this was not so is shown in the fuller version given by Haller in his *Emendationes*;[3]

> Numerous important journeys have provided much new material. Chief among these was the one made by Mr Dick, tutor to my sons, in company with Abraham Thomas, forest warder, in 1763. They went by way of Zürich, Kyburg, Coire, the Via Mala, the Splügen Pass and the valley of Fräele; thence over the Bernina Pass they reached the very high Septimer Pass, and went by way of the Furcula Pass, Mesocco, Bellinzona and the Borromean Islands to the Val Antigorio, and lastly over the Gries Pass and through the Valais they returned to me [at Roche], laden with the splendid finds which they had made on their very long journey....'

These included an *Alsine*[4] collected on the Bernina Pass, and *Galium parisiense*[5] near Formazza. Altogether the journey was a great success, and on 16 July 1763 Gesner wrote to Haller:

> '...Füssli and von Meis have returned delighted with their tour, and are warm in their praise for the kindness of the learned Dick. I have also received a letter from him full of nice feelings and gratitude. I have not yet studied all the plants collected on this tour, but there are some rare ones which I have never seen before.[6]

After he had made a study of them, Gesner compiled a list and enclosed it with the letter which he addressed to Linnaeus on 14 November 1763. This letter and the list are printed in the *Proceedings of the Linnean Society of London*, vol. **161**, 1949, pp. 236–40.

Haller's tenure of the post as director of the salt works at Bex came to an end in 1764 when he returned to live in Berne. Dick, meanwhile, wished to complete his education at a foreign university, and in view of the part which Haller had played at Göttingen, it is not surprising that that is where Dick went. In a letter[7] to Gesner, dated 27 October 1764,

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[1] *Historia Stirpium Helvetiae Indigenarum Inchoata*, Bernae 1768: 'Sic D. *Jacob Dick* V.D.M. pariter me curante, cum *Abrahamo Thomas* sylvarium custode, *Curiam, Spelugam, Clavennam, vallem Tellinam, juga Burmiensia, montesque Trone & Fräla, Berninam*, altissimum montem Septimum adiit, inde per *Furculam, Misaucum, Bellitionem*, alpesque *Grajas* & Valesiam *Rupem*, rediit, multis rarissimis plantis dilatus....'

[2] H. Dübi: 'Albrecht von Haller und die Alpen', *Deutsche Alpenzeitung* **8**, München, 15 Oktober, 1908, p. 39.

[3] Alberti de Haller ad Enumerationem stirpium Helveticarum emendationes et Auctaria vi, *Acta Helvetica*, **6**, 1767.

[4] *Epistolarum ab Eruditis Viris ad Alb. Hallerum scriptarum* Pars I, Bernae, **5**, 1774, p. 314, letter 262, Dick to Haller, 29 January 1767.

[5] *Ibid.* **5**, p. 317, letter 264, Dick to Haller, 10 April 1767.

[6] *Ibid.* **5**, p. 148, letter 199. Gesner to Haller.

[7] Sigerist, H. E.: 'Albrecht von Haller's Briefe an Johannes Gesner', *Abhandl. Königl. Gesell. Wiss. Göttingen*, n.f. **11**, 1923, p. 355, letter 291.

Haller wrote that Dick had already gone to Göttingen, and he added the information that he had obtained the living of Spiez on the Lake of Thun through the help of Baron von Ehrlach.

At Spiez Dick found himself in a region where there was much to be done by way of collecting plants. In a letter[1] to Haller dated 4 September 1766, Dick gave an account of his recent excursions, and said:

> I made a journey on 21 July into the Kienthal and its various nooks, such as the alps of Margofel, Hohkien, Sauss, Rothorn, Sulz, Glütsch, Egg, Lattrei and Suld. In these regions I found many elegant little plants, but nothing new. I made another journey on 5 August by way of Frutigen and Kandersteg into the Gasternthal and found a number of plants.

Dick then went on to make a request which is of considerable interest:

> If among the duplicates of the plants found at Zermatt and in the valley of St Niklaus in 1765 or in this year, there are any which I lack and which you would be kind enough to select for me, I should be most grateful for them.

Zermatt had first been visited by Haller's men, Pierre and Abraham Thomas, in 1763, 1764 and 1765, and in 1766 Zermatt had been visited by Bernard-Jean-François Ricou.[2]

On 21 December 1766 Dick sent Haller some specimens of *Alcine* which he had gathered in the precipice of Die Klaus near Kandersteg.[3] It is clear that Dick explored the valleys between the Kienthal and Lauterbrunnen very thoroughly, and it must have been a matter of great satisfaction to Haller for two reasons. In the first place, when Micheli du Crest had asked Haller for the names of the peaks of the Bernese Oberland for the panorama which he was drawing from his prison of Aarbourg, Haller seems to have made some mistakes and in particular to have applied the name Jungfrau to the Mönch.[4] He wrote to Micheli in 1755 saying that 'between the valleys of Lauterbrunnen and Gasternthal, there are some snow-covered regions, unexplored and inaccessible, to gain an idea of which it is necessary for somebody to visit the high mountains of the Kienthal'.[5] This was exactly what Dick did.

The other reason was that in 1742, Antoine-Noé de Polier de Bottens had gone with his horse from Kandersteg to Lauterbrunnen. An exaggerated and sensational account of this journey was published by M. T. Bourrit,[6] who made it appear that the route lay across the Tschingel Pass. This Haller very much doubted, and he suspected that it was in fact by way of the Hohthürli Pass, the hinder part of the Kienthal and the Sefinenfurke.[7] Dick seems to have been among the first who gave precision to the details of alpine topography in this region. Two years later, as Haller wrote[1] to Gesner on 14 June 1768, Dick acted as guide to Paul Dietrich Gieseke[2] on a journey to the glaciers of the Gasterthal.

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[1] *Epistolarum ab Eruditis Viris ad Alb. Hallerum scriptarum* Pars I, Bernae, 1774, 5, p. 284, letter 252. Dick to Haller.

[2] G. R. de Beer: 'Haller's Historia Stirpium', *Annals of Science*, **9**, 1953, pp. 39, 41, 42. G. R. de Beer: 'Mont Stok', *Alpine Journal*, **57**, 1949, pp. 181–3.

[3] *Epistolarum ab Eruditis Viris ad Alb. Hallerum scriptarum* Pars I, Bernae 1774, vol. **5**, p. 380, letter 259. Dick to Haller.

[4] G. R. de Beer: 'Haller's Historia Stirpium', *Annals of Science*, **9**, 1953, p. 26, letter 86.

[5] J. H. Graf: *Das Leben und Wirken des Physikers und Geodäten Jacques Barthélémy Michéli du Crest*, Bern: 1890.

[6] M. T. Bourrit: *Description des Alpes Pennines et Rhétiennes*, Genève, 1781.

[7] Haller maintained his interest in Alpine topography to the end. In October 1777, two months before his death, Haller received a visit from Karl Gottlob Küttner and spoke about Alpine travel. (*Briefe eines Sachsen aus der Schweiz*, Leipzig, 1785, **2**, p. 174.) It was presumably from him that Küttner learned of the route from Lenk to Leukerbad by way of the Ammerten Pass and Engstligengrat which Küttner followed in 1780. The possibility of passage by this route had been mentioned by Haller in his preface to Wagner's *Merkwürdige Prospekte aus den Schweizer Gebirgen*, Bern 1776, [1777], and a route almost similar was followed in September 1777 by Karl Viktor von Bonstetten, Johannes von Müller, and Jean Trembley. (G. R. de Beer: 'Une traversée de l'Engstligengrat en 1777', *Les Alpes*, Berne, **24**, 1948, p. 300. See also A. Wäber: 'Küttner's Übergang von der Lenk ins Leukerbad 1780', *Jahrb. Schweizer Alpencl.* **40**, 1904 (1905), p. 319.)

The Economical Society of Berne was founded in 1768, and very soon Dick was contributing to it. Having exchanged the living of Spiez for that of Bolligen in 1770, he compiled a memoir[3] on the economy of the Alps which was awarded a prize in 1771. In this work Dick concerned himself with answers to the following questions: what are the present state, the defects and the possibilities of perfecting the economy of our Alps and mountains? Dick discussed the conversion of alps into meadows, the extirpation of noxious plants and the propagation of useful ones, the care and upkeep of irrigation channels over the alps, the use to be made of superfluous rocks and boulders, the precautions to be taken against land-slides, economy in the use of wood, whether cows should be milked three times a day, whether it is more profitable to make cheese or butter, and whether butter should be salted.

He also contributed a catalogue[4] of plants of Switzerland which serve as nourishment for cattle. In order to obtain a standard list of names of plants in the local Swiss dialects, the Economical Society requested all corresponding societies, economists, doctors, apothecaries and botanists of Switzerland to collect the local names of the plants, useful or noxious in medicine or agriculture, with the proper names in Latin, German or French, together with a specimen of the plants if necessary, and to send them to either Mr Yth or to Mr Dick.

Dick was also the author of a list[5] of the rare plants that grow wild in the region of Spiez, and of a work on roses which remained in manuscript.[6] On 17 July 1774 Haller wrote[7] to Gesner that Dick had found a new *Ranunculus* hitherto unknown in the Swiss flora. The value of Dick's work as a botanist emerges also from the fact that Linnaeus's herbarium[8] contains thirty-one references to him, as shown in Appendix I.

It was therefore a very great shock when Dick died in 1775 at the age of 33. On 3 May of that year Haller confided[9] to Gesner that Dick had succumbed to a disease which had coagulated his blood in him. He left a widow and three daughters, a library and a herbarium.

The story now turns to Sir Joseph Banks and his herbarium, which is preserved in the British Museum (Natural History). Under the heading 'Herb. Helvet.', Banks made the following note:[10]

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[1] H. E. Sigerist: 'Albrecht von Haller's Briefe an Johannes Gesner', *Abhandl. Königl. Gesell. Wiss. Göttingen*, n.f. **11**, p. 413, letter 369.

[2] Paul Dietrich Gieseke, 1741–96.

[3] Jean-Jacques Dick: 'Mémoire sur l'économie des Alpes qui a remporté le Prix en 1771 par M. Jean-Jacques Dick, Pasteur de l'Eglise de Bolligue.' *Memoires et Observations recueillies par la Société Oeconomique de Berne*, 1771, pp. 59–114.

[4] Jean-Jacques Dick: 'Catalogue des plantes de la Suisse, qui servent à la nourriture du Bétail.' *Mémoires et Observations recueillies par la Société Œconomique de Berne*, 1774.

[5] J. Dick: 'Verzeichnis derjenigen seltenern Pflanzen welche in der Herrschaft Spiez freiwillig wachsen.' *Bernisches Magazin der Natur, Kunst und Wissenschaften*, **3**, 1779.

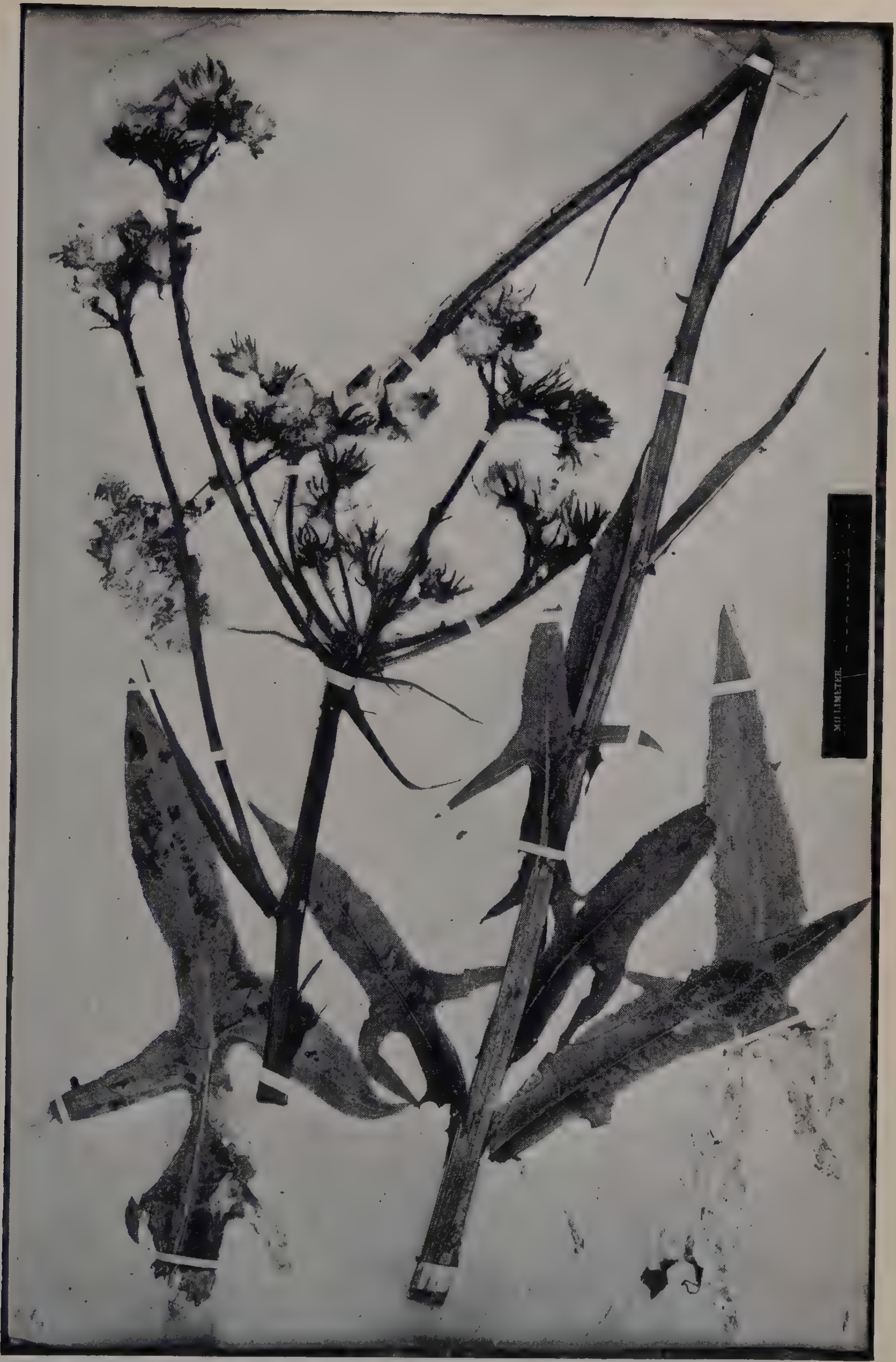
[6] G. R. de Beer: 'Edmund Davall, F.L.S., an unwritten English chapter in the history of Swiss botany', *Proc. Linn. Soc. Lond.* **159**, 1947, p. 57.

[7] H. E. Sigerist: 'Albrecht von Haller's Briefe an Johannes Gesner', *Abhandl. Königl. Gesell. Wiss. Göttingen*, n.f., **11**, p. 498, letter 494.

[8] *A Catalogue of the Linnaean Herbarium* compiled and annotated by S. Savage, London, 1945.

[9] H. E. Sigerist: 'Albrecht von Haller's Briefe an Johannes Gesner', *Abhandl. Königl. Gesell. Wiss. Göttingen*, n.f., **11**, p. 510, letter 509. On 17 August 1776 Werner von Lachenal wrote to Haller (R. Wolf: 'Auszüge aus Briefen an Albrecht von Haller', *Mitt. naturf. Ges. Bern.*, 1848, p. 242) from Basel: 'Ausserordentlich habe ich den Tod meines liebsten Freundes, des Herrn Pfarrers Dick, betrauert. Sollte sich Niemand mehr in der obern Schweiz befinden, mit dem ich einen botanischen Briefwechsel unterhalten könnte.'

[10] Published in 'Notes on the Banksian Herbarium', *J. Bot.* **40**, 1902, pp. 388, 389. There is also an entry in *The History of the Collections contained in the Natural History Departments of the British Museum*, **1**, 1904, p. 144. Among the names of botanists whose collections are in the Department of Botany appears: 'Dick ( ) 'Herbarium Helveticum'—collection of Swiss plants, purchased by Banks from Dr Pitcairn in 1775. See *J. Bot.* **40**, 1902, p. 388.'



Sonchus palustris L.

From specimen in Herb. Helvet. (of Dick) incorporated in the European collections at the British Museum (Natural History).

(*Facing p.* 324)

> In the year 1775, Dr Pitcairn was by a correspondent in Switzerland offered the purchase of a large herbarium, the collector of which was dead, and the whole to be sold for the benefit of the widow. As the Dr made no collection of dried plants he proposed it to me. I readily agreed, and a letter was returned desiring that if the price asked for it was reasonable it might be purchased and directly forwarded to me. It accordingly arrived consisting of 29 large pasteboard covers filled with plants loose on sheets of paper; the purchase money, charges of carriage, duty etc., of which amounted to £39. As yet however I have not been able to have the name of the person who collected it.

To this note, Robert Brown, who was Keeper of the Banksian herbarium, added: 'So far Sir Joseph. In Dryander's hand in pencil follows: "It was Dick".' These notes enable an explanation to be given of the reason why Britten and Boulger included Dick among the British Botanists. It was known that Dr Pitcairn,[1] in conjunction with Dr Fothergill,[2] had sent a botanist to Switzerland to make a collection of plants in the year 1775. This was also the year in which Dr Pitcairn was offered a collection of Swiss plants, and passed on the offer to Banks. The name of the collector was identified by Dryander as that of Dick. It is therefore almost certain that Britten and Boulger assumed that Dick was the name of the collector who had been sent out in that same year by Drs Pitcairn and Fothergill. It is now known that this collector was Thomas Blaikie.[3]

An echo of Dick's work is of interest to-day, as explained in the *Proceedings of the Linnean Society of London*, vol. **160**, 1948, p. 180. Dr Edouard Thommen commented on the interest attached to the inclusion of *Sonchus palustris* among the list of plants which Edmund Davall reported to William Curtis on 12 September 1787, because this species is lacking from the flora of Switzerland to-day. Davall's letter is printed in the *Proceedings of the Linnean Society of London*, vol. **159**, 1947, p. 140.

As I explained (in vol. **160**, 1948, p. 180) no specimens of *Sonchus palustris* can be found in the Smithian herbarium (in the collection of the Linnean Society of London) which is known to have contained the herbarium collected by Davall. It is therefore of the greatest interest that among the plants in the Dick herbarium, there is a beautiful specimen of *S. palustris* labelled in Banks's own handwriting as coming from 'Herb. Helvet.' which is, of course, the Herbarium Helveticum of Dick which he purchased. It is shown here on Pl. **23**.

Finally, a word should be added in explanation of a remark contained in a letter[4] from Jakob Samuel Wyttenbach[5] of Berne to Sir James Edward Smith dated 29 July 1813. In this letter, Wyttenbach describes how a botanical museum has been established at Berne, 'où nous possédons les Herbiers de Dick & Triboleth remplis de plantes de l'herbier de Haller'. This cannot have been Dick's main herbarium for the reasons stated above. Dr Friedrich Triboleth, Haller's executor, was known to have had a herbarium containing many of Haller's plants, and it is probable that it, or Haller's herbarium itself, contained many of Dick's plants. This would explain the attribution of the herbarium at Berne to Dick.

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[1] Dr William Pitcairn, M.D., 1711–91, F.R.S.

[2] Dr John Fothergill, M.D., 1712–80, F.R.S.

[3] Thomas Blaikie, 1750–1838. His journal was published under the title: *Diary of a Scotch Gardener at the French Court at the end of the 18th Century*, edited by Francis Birrell, London, 1931.

[4] G. R. de Beer: 'Some Letters from Jakob Samuel Wyttenbach to Sir James Edward Smith', *Annals of Science*, **6**, 1949, p. 113.

[5] Jakob Samuel Wyttenbach, 1748–1830, pastor of Berne.

APPENDIX I

Dick's plants in the Linnaean Herbarium[1]

(The numbers refer to the herbarium as listed in *A Catalogue of the Linnaean Herbarium* compiled and annotated by Spencer Savage, London, 1945.)

71.67a Scirpus Halleri. Dick. [Sm:] *Sc. supinus Davallii?* [C. B. Clarke:]☐Scirpus supinus, Linn., C. B. Clarke, Nov. 1887, //Hall. hist. 1344.
71.79 [Dick:]☐: *Scirpus quinqueflorus Hall. Hist. 1335.*
84.18 Dick. //Agrostis violacea. Hall. Syst. 1477.
84.46 *Agrostis aurea* [:m. Dick:] *Hall. 1498.*
85.19 canescens Dick. [Sm:] *cristata.* //Aira valesiana. Hall. Hist. 1445.
87.53 *nemoralis?* Dick. [:m.Sm:] *1468 Haller.* //Poa duriuscula Hall. Hist. 1486.
87.71 Dick. [Lindem. 1912:]☐ //Poa varia Hall. Hist. 1856. [*recte* 1456. G. de B.]
87.74 [Dick:]☐: *Poa juncea Hall. Hist. 1459.*
92.3 Dick. //Festuca varia Hall. Hist. 1439.
92.11 Dick. //Festuca montana Hall. Hist. 1438.
95.23 Dick. //Avena alpina Hall. Hist. 1500.
95.28 Dick. //Avena patula. Hall. Hist. 1489.
486.10 Dick. [Sm:] *angustissimum H*[*ort.*] *Kew. gelidum MS. B*[*anks.*]. //Epilobium alpestre Hall. Hist. 1005. [+Sm:] *1001.*
575.3 Dick. [Sm:] *mutata* //Saxifraga mutata Dick.
575.36 Dick. //Saxifraga biflora Hall. Syst. 981.
575.59 [Dick:]☐: *Saxifraga odorata Hall. Hist. 915.* [Sm:] *Dick tenera...planifolia...D. Don n.69.*
585.44 [Arenaria] laricifolia Dick. [Sm:] *vix A. lanceolata All*[*ioni*] *1715 nequaquam austriaca?*
585.60 Dick. //A[renaria] flaccida Hall. Hist. 863. [Sm:] *obtusifolia Allioni?*
603.16 Dick. [Sm:] *Stellaria cerastoides.* //Cerastium rhaeticum Hall. Syst. 899. [Sm:] *890. an varietas 890?*
603.32 Dick. //Cerastium uniflorum Dick.
919.4 [:??m.Locher, hortulorum 1771:]☐ *H*[*ippocrepis*] *multisiliquosa* [+Dick:] leguminibus pedunculatis confertis margine altero lobatis [Sm:] *H*[*erb.*] *Dick.*
988.58 Dick. [Sm:] *Herba alba Gesneri vallesiaca Allioni* //Artemisia Herba alba. Hall. Hist. 128.
996.50 Senecio alpinus. Dick. [Sm:] *an Cin*[*eraria*] *cordifolia Jacq.?* //Senecio alpinus Hall. Hist. 63.
1100.81 Dick. [Sm:][Carex] *foetida.* //Carex foetida Hall, Hist. 1355.
1266.27 [Dick:]☐: *Hypnum Dill. 41. f.50.* [+A. Berlin:] *rutabulum L.*
1266.97 [Dick:]☐: *Hypnum Halleri Hall. Hist. 1734.*
1266.108 [Dick:]☐: *Hypnum reflexum Hall. Hist. 1732.* [Schultz:] *Hypn*[*um*] *Stellatum.*
1266.109 [Dick:]☐: *Hypnum aristatum Dill. t.41. f.52.* [Schultz:] *Hypn*[*um*] *murale.*
1266.110 [Dick:]☐: *Hypnum trichoides Hall. Hist. 1751.*
1266.111 [Dick:]☐: *Hypnum rubiginosum Hall. Hist. 1753. Dill. n.60.*
1266.112 [Dick:]☐: *Hypnum pilosum Hall. Hist. 1778.* [Schultz:] *Dicranum virens.*

APPENDIX II[2]

Dick's plants in the Banksian Herbarium

The Dick plants in the Department of Botany in the British Museum (Natural History) have been incorporated in the European Herbarium, but are easily recognizable from the fact that the reverse side of each sheet is endorsed in Bank's own hand 'Herb. Helvet.'

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[1] In preparing this appendix I enjoyed the help of Dr A. Melderis of the Department of Botany, British Museum (Natural History), which it is a pleasure to acknowledge here.

[2] I wish to thank Mr A. W. F. Hales of the Department of Botany, British Museum (Natural History) for his assistance in finding the sheets of Dick's plants in the European Herbarium of that Department.

or 'Herb. Dick'. Some of them have Dick's own labels and the localities where he collected them. From the latter it is sometimes possible to assign approximate dates to the specimens from what is known of Dick's movements. Thus, the following are among the plants probably collected in 1762 when he was living with Haller at Roche:

Arabis coerulea [Dick:] Sisymbrium 28b. coeruleum foliis obligibus dentatis spica nutante Hall. Emend. IV. 46. in Alp. editiss. Darbon Fouli Gotthard.
Saxifraga biflora [Dick:] Saxifraga 18a. biflora. caule reptante foliis imbricatis ramis bifloris. Alp. Helv. M. Martinet, Fouli, Grandvire, [later addition:] Kienthal.
Bupleurum [Banks:] Bupleurum 2 stellatum L. & Crantz involucellis coadunatis universali triphyllo Crantz. Alp. Helv. Salanfe.
Ranunculus parnassifolius [Dick:] Ranunculus parnassifolius radicibus fasciculatis foliis cordiformibus imo caule obnupto. Hall. Emend. 3. n. 53. hab. in Alp. Alt. Fouli Jaman Ovanna [Bernard-Jean-François] Ricou.
Carex foetida [Dick:] Carex 4.1. foetida foetidus spica fusca conglomerata. H[all.] Hist. 1355 Darbignon, Fouli.
Gypsophila saxifraga perennis [Dick:] Dianthus 15a. Saxifragus. calycibus pelviformibus. Squamis calycinis 4 tis alternis majoribus. D[ick]. Gypsophila Saxifraga L. ob squamas calyc. Dianthi caracterum essentialem non ad gypsophilas referendum. in Helv. calid. arenos. Lausanam.
Lychnis Viscaria [Dick:] Lychnis 3 viscaria petalis integris. in Vallesia inter Diablay & Branson.
Silene armeria [Dick:] Silene 29 armeria. floribus fasciculatis fastigiatis foliis superioribus cordatis glabris. in Helvetia calidora. Rupe [Roche]. Vallesia.
Sisymbrium palustre [Dick:] Sisymbrium 4. a. riparium foliis pinnatis pinnis confluentibus, ectima rhomboidali, petalis calyce brevioribus. ad ripam Lacus Neocomensis [=Neuchatel] Grandson.

The following specimens were collected on the tour in the Grisons in 1763:

Silene rupestris [Dick:] Selene 31 rupestris floribus erectis petalis emarginatis calycibus teretibus foliis lanceolatis. in Alp. Mont. Helv. descens. Splugg. [later addition:] Gaster 1766.
Arenaria recurva [Banks:] Herb. Dni. Dick. Arenaria 12a recurva. Alsine petalis integris fol. subulatis, radicalibus congestis recurvis caulinis lanceolatis. Hall. Emend. I, 73. In Alp. Helv. Jugg. Borm. [=Umbrail Pass.]
Aretia alpina [Dick:] varietas villosissima ex Valle Tellina.

The following specimens date from 1766 and later years until 1770 during which time Dick was pastor at Spiez.

Aretia alpina [Dick:]. Aretia 1 alpina Lin. Androsace 8 alpina villosa scapis unifloris var. α glaberrima. *Obs*. fructus unilocularis quinque valvis, aut omnes Androsaces secundum inventorem Halleri Aretiae dicendae quod rectius, aut haec ad Androsaces referenda cum genere conveniat. Alp. Helv. Kienthal.
Astragalus alpinus [Banks:] Helvet. e Kienthal mons Helvetiae.
Anemone ranunculoides [Dick:] ad viam Wyler daneben Schwändi.
Saxifraga aizoon [Banks:] Helvetia: Kandelstäg [=Kandersteg] Dick.
Primula farinosa [Banks:] Helvetia Spiezmoos.
Gentiana bavarica [Dick:] Gentiana 11 bavarica. corolla quinquefida infundibuliformis serrata foliis obtusis. Alp. Helv. Bavar. Suev. Kienthal.
Avena pratensis [Banks:] Spietzberg Helvetiae.
Allium scordoprasum [Banks:] Kienthal. Dick.

Some of the plants in Dick's herbarium can be traced to other earlier collectors. One of the most interesting of these is the following:

Senecio cordifolius [Abraham Gagnebin:] Senecio de M. Haller, p. 730. Jacaboide des Alpes. Solidago *alpina* Linnaei Cassignete Plinii lib. 24. cap. 17. censuit Guilandinus. Dans le Pais de Hasli Laguerkraut. Gagnebin l'a vu 1° en 1726 sur la Dent de Jaman près la Vacherie, et près celle du Mont Pilate en 1763. et in udis du Hasliberg, du Scheideck près le Wetterhorn, et depuis Schindeleg à Einsidlen, à Altmatt, C[anton] de Schwitz, et dans l'Endlibuch. réussit fort bien au Jardin de la Ferrière [=Gagnebin's home]. [Dick:] Senecio 25*b*. alpinus. foliis cordate lanceolatis serratis, Hall. Hist. 63. Jüstis Thal hortulii in Alpis pinguibii pratis et circa casas pastorias.

The following specimens can be assigned to Werner von Lachenal (1736–1800) and Jean-Jacques Châtelain (1736–1822) on their journey of 1760 to the Italian lakes:

Arenaria alpina [Banks:] Helvetia circa Newstatt [=La Neuveville, home of Châtelain] & in Monte Generoso.

One specimen was obtained by Horace-Bénédict de Saussure:

Arabis ciliata [Dick:] Sisymbrium 25d. ciliatum. foliis lucidis ellipticis dentatis dentibus ciliatis. Hall. Emend. v., Cl Saussure in M. Salève Genevensi.

Finally, a group of specimens can be ascribed to the first visits to the valleys of Zermatt and of Saas, paid between 1763 and 1766 by Pierre Thomas, Abraham Thomas, and Bernard-Jean-François Ricou:

Anemone Halleri [Dick:] Anemone 5. a. incana foliis hirsutis pinnatis pinnis acute lobatis tubis caudatis. Hall. Emend. VI, n. 30, nova Planta habitat in M. Fluely Vall. Nicolai [=Zermatt valley].

Antirrhinum [Dick:] Antirrhinum 33B. Valesianum. foliis linearibus adscendentibus confertim spicatis calcare flore longiori: Hall. Hist. 337. ad pedem S. Bernhardi & Praborgne [=Zermatt].

Inula provincialis [Dick:] Solidago A. tomentosa. foliis tomentosis ovatis & semipinnatis. unissima Planta. M. Montemor Vales. [=Monte Moro Pass] Hallery.

APPENDIX III

The location of 'Im Loch'

The *Flora Alpina* published by Nicolaus N. Åmann,[1] raises an interesting point of alpine topography in the locality given for *Aretia alpina*: 'Loch altissimus mons Vallesiae', abbreviated into 'Vallesiae Loch', and described as lying in the 'Rhaeticae Alpes'. Linnaeus's *Species Plantarum* gives the locality of *Aretia alpina* as 'Habitat in Vallesiae Monte Loch'.

Linnaeus was not deeply versed in the topography of the Swiss Alps, and two questions therefore arise: where is 'Loch', and how did Linnaeus obtain the information that it was a locality for *A. alpina*. Dr A. Becherer[2] first drew attention to these problems, and put forward the suggestion that Linnaeus learned of 'Loch' from Albrecht von Haller in private correspondence. This locality is, however, not mentioned in Haller's *Nomenclator*[3] where, under number 616, the habitat of *Aretia* is given as 'in alpibus summis australibus Valesiae mediae & supremae'. 'Im Loch' does not appear, either, in the localities appended to *A. alpina* in Dick's herbarium. For the suggestion that Linnaeus learned of Loch from Haller, therefore, there is no evidence; and the key to the problem is to be found in the answer to the other question, the location of 'Loch'.

In the determinations which Linnaeus made of the plants in the Herbarium of Joachim Burser,[4] the locality of *A. alpina* is given as 'Loch Vallesiae', and there can therefore be no doubt that it was from Joachim Burser that Linneaus and Åmann derived their information.

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[1] N. M. Åmann: *Flora Alpina*, Uppsalia [1756].

[2] A. Becherer: 'Linnés Flora Alpina', *Les Alpes*, **22**, Berne, 1946, p. 98.

[3] Albrecht von Haller: *Historia Stirpium indigenarum Helvetiae inchoata* (Bernae), 1768. The locality is not given in either of Haller's large works: *Enumeratio methodica Stirpium indigenarum Helvetiae* (Gottingae, 1742); *Nomenclator ex Historia Plantarum indigenarum Helvetiae* (Bernae, 1769).

[4] Caroli Linnaei Determinationes in Hortum Siccum Joachimi Burseri, edited by S. Savage, *Catalogue of the Manuscripts in the Library of the Linnean Society of London*, Part II, 1937.

Burser was born in 1583 at Camenz in Upper Lusatia and became a pupil of Caspar Bauhin for whom he travelled through Switzerland, Austria, and the south of France. From Linnaeus's determinations in Burser's Herbarium it is clear that Burser travelled widely, for in addition to 'Loch Vallesiae', the localities of his plants include Passwang, Sion, Einsiedeln, Leukerbad, Coire, Lucerne, Altdorf, the Mythen, Schindellegi, Wallenstadt, St Niklaus (in the Zermatt valley), and the St Theodul Pass. Haller[1] further credited Burser with having visited Baden, Pfäfers, Disentis, the St Gotthard Pass, the Gemmi Pass, the Grand St Bernard Pass, and Mount Pilatus. These journeys must have been made before 1624, the year of Caspar Bauhin's death.

Burser made a herbarium and took it with him to Sora in Denmark where he became professor of medicine and where he died in 1639. But after the war between Denmark and Sweden when Sweden was victorious, Burser's herbarium was included in the reparations demanded, and taken to Uppsala, which is why Linnaeus was able to study it there.

The text of Burser's herbarium itself has been published by H. O. Juel,[2] and it shows more detail than the shorter list which Linnaeus made. In particular, the locality of *A. alpina* in Burser's herbarium is given as 'In altissimo Vallesiae monte, im Loch dicto'. The little word 'im' prefixed to 'Loch' supplies the key to this elusive locality. In his *Itinera Alpina*,[3] Johann Jacob Scheuchzer described this place as '*Ad laevam* Rhodani *e regione fere* Ulricae *quondam Coenobium Monacharum erat* (*Im Loch* nunc appelari testatur *Stumpf*).' And in his '*Schweytzer Chronik*, Johann Stumpf[4] wrote: 'Zwüschen den jeyztbenenten dörffern/Gestelen und Münster/vor Ulrich ober/auf der lincken seyten gegen Mittag/ist gelegen ein Frawenclosterlin/jetzt genent im Loch/ein Schwesterhausz/nit grosses wesens/ist in der zeit vergangen ausz mangel der personen/auch notturfftiger narung/und von wegen der wilden gelegenheit.'

'Im Loch' lies therefore between Obergestelen and Münster, opposite Ulrichen to the south, on the left side of the Rhone, at the entrance to the Eginental, through which the path leads to the Gries Pass and the Nufenen Pass. To this day, this place is designated on the map by the name 'Im Loch'.

Two further points arise for consideration. Im Loch lies at the bottom of a valley, and it may therefore appear curious that Burser should speak of it as In altissimo Vallesiae Monte, and Åmann as altissimus mons Vallesiae. I believe the explanation to be that Im Loch is in what is called the Upper Valais; *Vallesia suprema* Haller called it. This designation of great height became transferred from the district of the Valais to the locality of Im Loch, in accordance with a predilection for extreme exaggeration of altitude which no early author was able to resist.

Secondly, it may be asked why Åmann placed Im Loch among the 'Rhaeticae Alpes'. Here again the answer is to be found in Burser's herbarium where the Gotthard itself is described as 'Rhaeticae'. Im Loch is at the western edge of the Gotthard Massif and was therefore included under the term Rhaeticae which, in early times, had a much wider extension than the Rhaetia or Grisons of the present day.

Finally, it may be noted that this little paper-chase of a place-name has emphasized an important fact, that in Burser's herbarium, which was classified according to Caspar Bauhin's principles, Linnaeus had almost direct access to the work of his great Swiss predecessor Bauhin.

[1] Albrecht von Haller: *Historia Stirpium*: preface.

[2] J. O. Juel: *Symbolae botanicae Uppsalienses*, II, 1, 1936.

[3] J. J. Scheuchzer: *Itinera Alpina*, Lugduni Batavorum, 1723.

[4] Johann Stumpf: *Schweytzer Chronik*, Zürich, 1608.

Appendix IV

Swiss Herbaria in Great Britain

Many other Swiss Herbaria have undergone the same fate as that of Johann Jacob Dick and are now preserved in British museums and learned societies. Laurent Garcin, F.R.S. (1683–1752) and his son Jean-Laurent Garcin (1733–1781), who lived at Cottens near Nyon on the Lake of Geneva, were both botanists of distinction. The latter was a poet in addition, and literally caught his death of cold after an excursion to Chamonix. 'En 1781, il revint très échauffé d'une course dans les Alpes du Valais et de la Vallée de Chamouny: une fièvre bilieuse ne tarda pas à se déclarer et malgré tous les secours de l'art, il y succomba le 9 novembre à l'age de 48 ans.' The biographical note[1] then continues: 'Après sa mort, son magnifique herbier de plantes indigènes, ainsi que ses propres manuscrits, et ceux de son père qu'il avait conservés, furent malheureusement enlevés à la Suisse, et passèrent en Angleterre dans les immenses collections du lord comte de Bute, qui s'était hâté d'en faire l'acquisition'.

Many plants of the Garcin Herbarium are preserved in the European Herbarium of the Department of Botany of the British Museum. Many more (621) are preserved in the National Museum of Wales at Cardiff. The sheets bearing Garcin plants are recognizable by the words 'Herb. Helvet. John Earl of Bute legit Garcin', on the back, and a reference to Haller's *Historia stirpium* (1768) on the front, but mostly without localities.[2] The plants were attached to the sheets by paper strips affixed with red sealing wax.

A letter[3] from Jean-Laurent Garcin dated 27 August 1778 refers to a botanical journey made in that year through the Valais in company with Abraham Thomas (Dick's companion in 1763) and states that he was actually engaged in writing an account of the journey. This manuscript must be one of those referred to above, none of which has yet been traced.

John Stuart, 3rd Earl of Bute (1713–92), was in correspondence with Haller, who frequently referred to his generosity in his letters[4] to Johann Gesner. On 22 June 1762: Bute had sent Haller John Hill's *System of Vegetable Generation*; 25 October 1763: Bute is helping with a volume of Hill's work so that he may send it to his friends. In 1769 Bute himself visited Haller, who wrote to Gesner, 8 February, that Bute discourses much on the structure of mountains; he was on his way back from the Pyrenees, and showed great affection for natural history.

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[1] Printed in *Le Conservateur Suisse*, Lausanne, **13**, 1857, p. 83. There is an interesting note on Jean-Laurent Garcin in the Diary of Thomas Blaikie for 15 August 1775 (*Diary of a Scotch Gardener*, edited by Francis Birrell, London, 1931, p. 72:

'...From this place [Aubonne near the Lake of Geneva] I went and called upon a curiouss Gentelleman that has a house in the neighbourhood, here I was well receved; this Gentleman pretends to be a great Botanist and told me that he had been at St. Genix to see my collection of plants I had colected with which he was well pleased; at that time he entended to publish a work upon the Gramins; he told me that his father was a great man and belonged to the Royalle Societty of London and showed me his name in the *specie plantarum* of Linne which plant he said was named after his father which is the *Garcinia* but the plant before that is the *Blakea* which he asked me if it was not named after my father; I told him surement so we concluded we was very nearly related in the Linnaean System and so we must go together to the Mountains and spend a day or two, as I told him there was severall plants toward the Dolle which although he had botanisd all thereabouts he had never found; after dinner we went to St Cerge [St Cergue].

'*August 16.* Went in the morning with Mr Garcin to Mont Pierre Olivier found but little new; went to the north of this Mountain to a little Lake [Lac des Rousses] which Mr Garcin wanted to see there being several plants especially the *vaccineums* and *Andromeda* which grows there which he had never found. Returned round the Dolle and came and lodged at St Cerg.

'*August 17.* Sett of early in the Morning with Mr Garcin to the Mountains but he being so much fatigued with the Road I had taken him yesterday that he could not continue a second days marche so we parted...'

[2] A specimen of *Viola calcarata* bears the locality 'Branvaux'.

[3] *Conservateur Suisse*, **13**, pp. 333–334.

[4] Sigerist: 'Albrecht von Haller's Briefe an Johannes Gesner', *Abhandl. Königl. Gesell. Wiss. Göttingen*, **11**, 2.

On 5 April 1771 Haller wrote to Gesner that Lord Bute had sent him some books including a very rare anatomical work by Giambattista Canano. On 25 October 1771: 'I have received a royal gift from Bute who has surpassed all princes by his munificence.' There can be no doubt that the relations between Lord Bute and Swiss men of science were close and cordial.

Lord Bute's son John Stuart, Lord Mount Stuart (afterwards 4th Earl and 1st Marquess of Bute, 1744–1814), was in Geneva shortly after Jean-Laurent Garcin's death. This is known from a letter[1] addressed by Isaac Pictet de Pregny (Lord Mount Stuart's host) to Lord Hillsborough dated 12 December 1781. Pregny is only ten miles from Cottens, and Garcin had died one month previously. It was presumably then that Garcin's herbarium and manuscripts were acquired. The former has now been traced. A small number of printed sheets, apparently forming part of the *Botanical Tables* published by the Earl of Bute in 1785, were found[2] in Cardiff Castle, but not Garcin's manuscripts, and it is very much to be hoped that they may yet be traced.

Some of Lord Bute's collections must have been given to Sir Joseph Banks, for while the majority of Garcin's plants preserved in the Banksian Herbarium are on their original sheets, some of them have been transferred to others which bear the words 'Lord Bute Herb.' in Banks's handwriting.

A third Swiss herbarium to come to England is that of Daniel-Moise Favrod (1742–83), schoolmaster of Château-d'Oex. He is referred to by Charles Victor de Bonstetten who was bailiff of that district in 1779, and whose work *Briefe über ein Schweizer Hirtenland* was translated into English by Mr Randolph.[3]

> I cannot here pass by my friend Favrod, who, amidst domestic cares, and those more laborious ones of a schoolmaster superadded, has pursued the study of botany with such unwearied diligence, that one cannot see him without regretting his poverty, and the time that his industry is deprived of. He has exceeded the number of Haller and Linnaeus [i.e. the number of alpine plants listed by them]; has translated many plants into his little garden at Oesch [=Château-d'Oex]; searched into their nature and properties; and discovered various salutary effects from them relative to the cattle.

The remarks about Favrod's poverty are confirmed by his appeal in 1774, to have his salary raised; it was 75 petits écus, or £9 a year. He was promised a bonus of £2 the following year.[4] The remarks about Favrod's skill as a botanist are borne out by the testimony of Jacob Samuel Wyttenbach, already quoted in these *Proceedings*.[5] His herbarium was described by W. F. Drake and by Sir James Edward Smith, and characterized as 'very copious and well-chosen'. After his death, it was bought by Edmund Davall (1763–98), the young Englishman who settled at Orbe.

A fourth herbarium to consider was that of Louis Reynier (1762–1824), F.M.L.S. (1788) who sold it to Davall in 1789 when he abandoned botany and took to politics. It is spoken of in equivocal terms both by Davall and Smith, although it contained many plants of interest.

Davall's own herbarium was highly praised by Smith 'not only for the extreme beauty, variety and abundance of the specimens, whether collected by himself or his friends, but also for their authority. In every difficult case he consulted the son of the great Haller, as well as Prof^{r} La Chenal, Mr Wyttenbach of Berne, & Mr DuCros, & had specimens with their authority of almost every Swiss plant.' When Smith received Davall's herbarium by bequest, he also received Favrod's and Reynier's. A catalogue of the Smithian Herbarium is in course of compilation, and it will no doubt throw much light on the collectors and localities of these Swiss plants.

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[1] Preserved in the Public Record Office F.O. 74/1.

[2] From information kindly supplied by Mr H. A. Hyde.

[3] *Observations on the present State of Denmark, Russia, and Switzerland.* London, 1784, p. 252.

[4] Eug. Roche: *Chateau d'Oex et le Pays D'Enhaut au XVIII siècle.* Chateaux d'Oex, 1913.

[5] *Proc. Linn. Soc. Lond.* **159**, 1947, pp. 62, 63.

The sixth Swiss herbarium to make its way to England was that of Jean-François-Théophile Gaudin (1766–1833), pastor of Nyon, and therefore close neighbour of Garcin, Davall and DuCros. Gaudin's work *Flora Helvetica*, published between 1828 and 1836, in eight volumes, was based on enormous material, collected in the course of many journeys in Switzerland and neighbouring countries. He bequeathed his herbarium to his pupil Joan Gay (1786–1864), at whose death it was offered for sale at the price of 1500 francs (£60). It was bought by Sir Joseph Dalton Hooker, and brought to Kew where it remained until 1878. In that year W. Barbey visited Kew in connexion with his work on *Epilobium*, and took the opportunity of asking Hooker whether there was any chance of his parting with Gaudin's herbarium, and under what conditions. Hooker replied that he refused to sell it, but that he would be glad to present it to the Canton de Vaud.[1] It was received by the Botanical Museum at Lausanne in November 1878, where it forms the nucleus of the cantonal collection. In return a herbarium of Swiss plants was collected by L. Favrat at Barbey's expense and sent to Hooker at Kew.

There is a curious fact about botanists who have collected and travelled in Switzerland: their habit of writing and publishing guide-books anonymously. Louis Reynier was the author of *Le Guide des Voyageurs en Suisse, précédé d'un Discours sur l'état politique du Pays*, Paris 1790, the attribution of which has only recently been established.[2] The study of botany involves the collecting of new plants which, in turn, is dependent on travel which both demands and provides topographical information. It is therefore not surprising that others besides Reynier should have written guide-books; but what is curious is that they, too, should have published their works anonymously. Another example is that of Thomas Martyn, F.R.S., author of *Sketch of a Tour through Swisserland*, London, 1787. Yet another example is that of the second French edition of J. G. Ebel's *Manuel du Voyageur en Suisse*, Zurich, 1810. Volume 1 of this work, paragraph 17, on page 251, reveals that the translator was the author of *Étrennes de Flore pour l'an* 1804, published at Lausanne, and he was Jean-François-Théophile Gaudin.

It looks as if these men of science felt some sense of shame in publishing works that were outside the scope of their professional activities; and this supposition finds support in the fact that when a science was mentioned in the title of the work, its authorship was acknowledged. Louis-Joseph Murith did not hesitate to put his name on the title-page of *Le Guide du Botaniste qui voyage dans le Valais*, Lausanne, 1810; and volume 7 of Gaudin's *Flora Helvetica*, Zurich, 1833, is really a guide-book. They need not have felt so diffident, for a good knowledge of local topography is part of the technique of many branches of natural history; and the topography of the Swiss Alps owes much to botanists: Pierre Thomas and his son Abraham in the Alps of Vaud and the valleys of Zermatt, Saas, Hérens, and Ferret; Bernard-Jean-François Ricou at Zermatt; Johann Jacob Dick in the Kienthal.

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[1] L. Favrat: Note sur les Herbiers Gaudin, et Hooker, *Bull. Soc. Vaud. Hist. Nat.* **17**, 1880, p. 1.

[2] It was considered possible by A. Wäber in his *Bibliographie der Schweizerischen Landeskunde* but very uncertain. It was established by me (G. R. de Beer: 'Les Botanistes et les Alpes', *Die Alpen*, Bern, **23**, 1947, p. 132).

The Marine Algae of New Zealand. Part I. Myxophyceae and Chlorophyceae.

By V. J. CHAPMAN, Professor of Botany, Auckland University College.

(With Plates 24–50[1] and 153 Text-figures)

[Read 6 May 1954]

INTRODUCTION

It is some years since Laing published his list (1926) of the seaweeds of New Zealand. Our knowledge of these plants has been considerably extended since then, and a critical examination of the material has been desirable for some time. This is all the more important because it is likely that major advances in the knowledge of algae, both in respect of structure and reproduction, will come from a study of south Pacific and Antarctic species.

This contribution is the first of three in which a detailed revision of the New Zealand marine algae has been undertaken. The present work deals with the Myxophyceae and Chlorophyceae. The second part, which is being prepared by Mr V. W. Lindauer, will deal with the Phaeophyceae, and the third part will be concerned with the Rhodophyceae.

The work has only been rendered possible by the accumulation of much material and literature together with access to herbaria. A considerable debt is due to the Council of Canterbury University College for the 5-year loan of the important Laing Collection. I am also grateful to the Research Grants Committee of the University of New Zealand for a grant that enabled me to visit herbaria in Europe, especially to examine specimens of the genera *Enteromorpha* and *Ulva*. The extensive herbarium of the Plant Research Bureau has also been available, and Miss L. B. Moore has provided much assistance and criticism for which I am very grateful. I would also thank Mr Lindauer for access to his extensive private collection. Inspection has also been made of the smaller collections in the Dominion Museum and the Auckland Institute: to the Directors of both these museums I express thanks. There is also a debt to my former technical assistant Miss S. Baker who has been responsible for the photographs. These have been selected to show either the types of new species or the habit of certain species.[2]

Recognition of assistance with various divisions or families is expressed in the relevant places. It is not expected that these contributions will represent the final picture for New Zealand. There are many parts of the coast where very little collecting has been carried out, and work in such areas may bring further new species to light and will certainly extend the range of others.

Apart from the four major algal groups, there are marine diatoms and marine members of the Xanthophyceae, Cryptophyceae and Chrysophyceae. Our knowledge of these is at present so meagre that it would be premature to attempt to list them.

Before proceeding to the detailed systematic account, some brief observations will be made in the next few pages on the distribution of marine algae and the various types of habitat that they occupy. This section owes much to collaboration with Mr V. W. Lindauer.

GENERAL FEATURES

The normal beach is dominated by red and brown seaweeds, the green algae being most frequent where there is an inflow of fresh water. The blue-green algae commonly form gelatinous colonies or membranous sheets on dripping rocks, on the underside of boulders, in caves, or on the mud of mangrove swamps and salt marshes. The individual plants of the blue-green algae are not visible to the naked eye whereas those of the other groups usually are.

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[1] *Editor's Note.* Owing to the poor state of preservation of some of the specimens, the author was unable to supply better illustrations. These have been reproduced as faithfully as their quality permits.

[2] My thanks are also due to the Council of Auckland University College and the Research Grants Committee of the University of New Zealand for financial assistance towards the publishing of this paper.

Colour can normally be employed as a guide for the initial classification of seaweeds, but there are occasions when it may be deceptive. Some of the red algae under shade conditions tend to be brown (e.g. *Catenella*, *Gracilaria*), or when fully exposed to sunlight they become greenish (*Porphyra columbina*, *Gelidium* sp., *Gigartina chapmanii*), whilst some of the brown algae may also appear greenish (*Ectocarpus*, *Dictyota*). However, the microscopic structure of the plants is then sufficient to enable one to determine the group to which the particular plant belongs.

Types of shore

The ardent collector finds the most fruitful field on the rocky shore, though even here degree of exposure or protection makes a considerable difference. Thus the rocky shores of the Tasman coast are often richer than the more protected Pacific shores, because the prevailing westerly wind makes for rougher conditions on the west, and the harbours of the east are generally muddy. Apart from protection and exposure on rocky shores there is also the nature of the beach. A bed of rough-surfaced, horizontal or gently sloping rock below low water or just above it, especially if pocketed into rock pools or submarine pools, or if dissected by gullies, often becomes a veritable garden; many seaweeds, however, especially those of the conspicuous shoreline associations, prefer more or less vertical rock faces. For these reasons a more or less uniform, flat, rocky shore (e.g. Narrow Neck, Stanmore Bay) is not so rich in species as an irregular dissected shore (e.g. Bay of Islands) because the latter provides a wider range of habitat.

Rocky shores can be divided usefully into five types:

(1) Gently shelving towards and below low water.

(2) Horizontal platforms in terraces, ending either gradually in shallow water or abruptly over deeper water.

(3) More or less horizontal platforms cleft into wide or narrow, deep or shallow channels connecting with the sea.

(4) Scattered rock-masses emerging from a floor of sand, shingle or mud either in the littoral or below.

(5) High, flat or pinnacled rock-masses raised above half-tide, level throughout and extending to low-water or below.

Of these (2) and (4) generally bear rich harvests, especially if facing the open sea or in other situations where the water is clean and well aerated and in sufficient motion. It must be remembered, however, that some algae prefer still, turbid waters or even an admixture of fresh water.

There may also be differences in the geological composition of the rock. Normally this has little effect upon algal vegetation but it has been found that excess of chalk does produce considerable changes in a flora. A soft rock, such as sandstone, may prevent a number of species from becoming established because of the erosion that takes place. An area of soft sandstone rocks therefore is likely to be poorer in species in comparison with a similar area of hard rock.

Rocky shores, however, are not the only type of shore on which algae can be found. Bouldery or pebbly beaches are not uncommon, though the amount of vegetation they carry depends on the size of the boulders. If they are of such a size that they are moved too often by the waves, as on the Taranaki coast, considerable scour is set up and algae have little opportunity to become established. Large boulders, however, may be covered with a rich vegetation. Such a coast may possess a rich sublittoral flora, samples of which are thrown up on the beach after storms.

Sandy beaches are usually bare of algae, though occasionally one may find discolorations of the sand caused by the local abundance of some minute alga (e.g. 90-Mile Beach). In other places occasional sunken pebbles may provide a substrate for a few plants which grow through the sand covering. The cast or drift weed on a sandy beach should not be neglected, because it may often provide a clue to the existence of a rich bed of algae growing submerged off the shore, either on rock outcrops or else on a bed of *Lithothamnion* or shell.

Estuaries and harbours are also worthy of investigation because, although they may have only a pebbly, sandy or muddy shore, the conditions are quieter and this enables some species to grow that otherwise would be absent. Often the calm water, its higher temperature and lower aeration, as well as the admixture of fresh water from rivers, will influence the growth of plants which, normally inhabiting the open coasts, occasionally invade these quieter and more sheltered situations. It may be that they become stunted, or develop more delicate, broader fronds, or that they become excessively branched. Such plants are regarded as representing ecological modifications and are termed *ecads*. Similarly, one should never omit to examine the piles of wharves, floating logs or drifting timber.

Other habitats that are profitable, though usually neglected, are salt marshes and mangrove swamps. Here one may find peculiar free-living forms and a wide range of Myxophyceae (blue-green algae). The Myxophyceae are not spectacular and it is often difficult to secure sufficient material for a herbarium sheet; but this is not really a valid reason for neglecting them. Interesting species of *Enteromorpha* may also be found in such places, and some algae are more or less restricted to the erect roots of the mangrove.

Terminology

Different authors have varied in their treatment of the shore. At present there is a lack of uniformity in respect of what is meant by the littoral and sublittoral. In this work the littoral is regarded as that part of the beach between high- and low-water marks of ordinary spring tides. The supralittoral will be that part of the beach above high-water mark of ordinary spring tides up to the lower limit of land vegetation on open shores, or up to extreme high-tide mark in the case of mangrove swamps and salt marshes. On exposed coasts it will include what is known as the '*splash zone*', a region occupied by algae above their normal level because of the amount of spray and splash. This varies from place to place, but on the west coast, e.g. Piha, it may be considerable (20 ft.). The region between low-water mark of o.s.t. and e.l.s.t. can be termed the sub-littoral fringe, and then below extreme low-water spring tides there will be the sub-littoral where algae are permanently submerged.

Rarely submerged	Supra-Littoral or splash zone; above high-water o.s.t.[1]
Emerged and submerged regularly twice daily	Upper-littoral; between high-water o.s.t. and half-tide mark
	Lower-littoral; between half-tide mark and low-water o.s.t.
Emerged only at spring tides	Sub-littoral Fringe; between low-water o.s.t. and e.l.s.t.[2]
Permanently submerged	Sub-littoral; below e.l.s.t.

The brown algal population of the *upper-littoral* is very limited, but green, blue-green and red seaweeds are present to a greater or lesser extent, according to the environment. In this region some plants, especially the Chlorophyceae, are light-seeking and flourish on damp rock, in cracks, shallow runnels, water-filled pockets or rock-pools; others seek the shade, inhabiting only the shady side of rocks, or are present under ledges. In caves green and red algae often line the walls in somewhat regular series, but the browns are seldom represented.

All seaweeds living in this zone are exposed to the atmosphere for many hours each day without immersion. In regions north of Auckland, where low water occurs during the hottest hours of the day and the coldest hours of night, plants must be able to withstand extremes of temperature, desiccation and frequent drenchings of rain. In Stewart Island and the southern part of the South Island the same conditions exist, with the additional factor of frost.

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[1] o.s.t. = Ordinary Spring Tide.

[2] e.l.s.t. = Extreme Lowest Spring Tide.

In the *lower-littoral*, from half-tide mark, the moderate-sized brown algae are much more numerous together with many red algae, both on the emerged substratum and in the tide-pools where sub-littoral species establish themselves, especially towards low-water mark.

In New Zealand the *sub-littoral* fringe, uncovered for a short period at major spring tides, is Nature's favoured spot for the display of the Phaeophyceae, although numerically they predominate in the zone below.

On the sea-floor, in the *sub-littoral fringe*, seasonal assemblages of the smaller brown and red algae establish themselves in plenty according to the nature of the shore, but the constituent units vary from beach to beach.

The sub-littoral zone is the true home of the Laminariales but deep-water Fucales of the family Sargassaceae also abound, whilst one also finds here the New Zealand species of the green algal genus *Caulerpa*.

Ecology

Sooner or later the student of the sea shore will come to study the algae as communities: in other words, study their ecology. The manner in which certain algae and animals are restricted to definite zones cannot but impress itself upon the observer, and definite communities can be recognized. Here again there may be difficulties in terminology. In the past algal ecologists have tended to adopt the terms used by land ecologists, but they have given such terms quite different meanings. This has been particularly true of the term 'association'. Logically there are two possible courses: either to use new terms or else to use the existing terms and to adhere to their original meanings. The present author believes the latter to be the correct alternative and recommends its adoption. In such a case the definitions of the various units can be given as follows:

Association. A community of constant form and physiognomy and dominated by two or more species.

Consociation. A community similar to the above, but smaller, included within the association and dominated by a single species.

Society. A local community in which one of the subsidiary species is locally dominant.

Clan. A minor community.

Facies. A variation of an association.

The horizontal extension of any of these communities forms a *belt*, whilst a vertical transect down the shore and including a number of these units can best be described as an *association complex*.

Formation. A major unit comprising one or more associations.

The definitions given above refer to vegetation that is in equilibrium with the environment: this is known as *climax vegetation*. In the case of salt marshes and mangrove swamps dynamic change is taking place, and as the land gradually becomes higher one community is replaced by another. Such relative instability in the communities is recognized by using a different termination so that we talk of *associes*, *consocies*, *socies* and *family*.

If the investigator is not certain of the status of any piece of vegetation under investigation then it should be termed a 'community' until such time as its status is apparent. For the guidance of those who are not familiar with algal ecology the following examples of the application of the above terminology may be quoted:

Formation	Balanoid formation
Association	(1) *Chthalamus-Saxostrea* (barnacle-oyster) (2) *Chthalamus-Apophloea* (barnacle-red seaweed)
Consociation	*Apophloea*
Society	*Microdictyon*
Clan	*Lyngbya* (on Coralline)
Facies	*Vermicularia* (worm)

These examples illustrate a further point—namely, that it is not really possible to study marine algal ecology without considering the animal denizens also, because they may in certain cases be more important than the plants.

ZONATION

The study of zonation on New Zealand shores is still more or less in its infancy and much further work remains to be done.[1] On rocky shores the fundamental zonation is represented by four main zones:

(1) *Melaraphe–Lichina* association, which is the New Zealand community of the *Littorina* formation found in other parts of the world. *Melaraphe* is a small mollusc closely allied to *Littorina*, and *Lichina* is a maritime lichen which forms black patches on the rocks. This community is commonly the uppermost one.

(2) Balanoid formation. This occupies the major portion of the littoral and exists in a number of different associations which vary from place to place. There is a greater variety on exposed coasts where various red algae, such as *Pachymenia* and *Gigartina* play a part. On the east coast of the North Island the dominants are one or more of the barnacles (*Chthalamus* sp.), *Elminius plicatus*, the rock oyster, the worm *Vermicularia* and the red alga *Apophloea*.

On protected portions of the east coast of the North Island the balanoid formation is succeeded usually by:

(3) *Corallina–Hormosira–Leathesia* association. In this the brown alga *Splachnidium rugosum* in certain parts of New Zealand forms a seasonal society whilst the green *Codium adhaerens* (p. 487) may form a permanent society.

This association does not occur on the more exposed west coast where it is replaced in the North Island by *Pachymenia* and *Gigartina* associations.

(4) Large brown algal formation. This has been termed the sub-littoral fringe, but our term seems better so far as New Zealand conditions, and possibly conditions elsewhere, are concerned. It exists in a number of associations and consociations which vary from place to place. On the west coast there is the *Durvillea* (bull kelp)–*Mytilus* association, on the east coast of the North Island there is the *Carpophyllum–Ecklonia* association, whilst to the south there is the *Macrocystis* consociation (Cook and Foveaux Straits) and a *Lessonia* consociation.

Table 1 summarizes some of the more important rock zonations, together with the specific localities from which they were recorded.[2]

Apart from the communities on rocky shores there are additional communities specific to other types of shore. Thus in the mangrove swamps of the North Island there is a free-living *Gracilaria* consociation which appears to occupy levels near the upper limit of the mangrove. Lower down a *Bostrychia–Catenella* association will be found on the trunks and pneumatophores of the mangrove, whilst a seasonal *Monostroma* society can usually be found in the small drainage creeks.

Among the plants of the salt marsh one can find societies of *Lola tortuosa*, *Rhizoclonium* and species of *Lyngbya*, *Oscillatoria* and *Nostoc*, the latter requiring a careful search as otherwise they may be overlooked.

ROCK POOLS

Rock-pools are Nature's aquaria, often of the greatest interest and crammed with unexpected and exquisite beauty. They may be either shallow or deep, and are found at all levels of the littoral. They are often classified according to the type of bottom, e.g. rock, sand-covered rock or coralline. Near low-water mark they frequently harbour species which could not otherwise withstand the alternation of tide and exposure. Here such

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[1] Papers already published are those by Oliver (1923), Cranwell & Moore (1938), Chapman (1950), Beveridge & Chapman (1950), Dellow (1950), Carnahan (1952).

[2] It is hoped later to write a fuller account of the ecology of New Zealand shores.

TABLE 1

	Piha			Anawhata[1]	East coast[1] Auckland	Poor Knights[1]	Rangitoto	Narrow Neck	Russell
	Moderate shelter	Moderate exposure	Strong exposure						
Littorina formation	Lichina–Melaraphe	Lichina–Melaraphe	Lichina–Melaraphe	Melaraphe–Lichina	Melaraphe + Lichina or Bostrychia + Myxophyceae	Melaraphe + Verrucaria + Myxophyceae	Melaraphe–Lichina Catenella–Caloglossa Myxophyceae	Melaraphe–Calothrix Bangia–Porphyra Enteromorpha–Gelidium–Volsella	Melaraphe–Lichina + Gelidium or Bostrychia
	Bostrychia arbuscula	Bostrychia arbuscula	Bostrychia arbuscula						
Barnacle formation	Chamesipho columna	Chamaesipho columna + C. brunnea + Gelidium pusillum	Chamaesipho columna	Chamaesipho brunnea	Chamaesipho brunnea	Chamaesipho brunnea	Chamaesipho–Apophloea C. brunnea Saxostrea	Chamaesipho–Elminius + Modiolus Saxostrea	Chamaesipho–Apophloea Saxostrea
	Elminius Gigartina alveata Volsella	Elminius Volsella Gigartina alveata		Chamaesipho columna Apophloea Gigartina alveata	Chamaesipho columna Elminius Apophloea or Saxostrea	Apophloea–Elminius	Scytothamnus australis Vermicularia Elminius–Modiolus	Scytothamnus australis Hermella–Vermicularia	Scytothamnus (protected areas only) Hermella–Vermicularia
					Hormosira		Hormosira	Hormosira–Corallina	Hormosira–Corallina
Lower littoral mixed algae formation		Pachymenia or Hermella or Mytilus	Durvillea + Corallines	Pachymenia or Durvillea	Hormosira + Corallines	Novastoa–Corallines	Corallina–Hormosira + Codium adhaerens Splachnidium Cystophora	Corallina–Hormosira + Codium adhaerens Splachnidium Caulerpa sedoides	Pachymenia or Hormosira–Corallina
	Gigartina atropurpurea	Gigartina marginifera			Xiphophora or Mytilus	Xiphophora	Xiphophora		
Brown Kelp formation	Schizymenia Cladhymenia	Vidalia Melanthalia Pterocladia	Durvillea	Durvillea, Carpophyllum or Corallines	Carpophyllum spp. Ecklonia	Carpophyllum elongatum Lessonia	Carpophyllum–Ecklonia Mytilus-tunicate	Carpophyllum–Ecklonia	Xiphophora Carpophyllum Ecklonia

[1] Data from Cranwell & Moore (1938). The author is indebted to research students at Auckland University College for much of the above data: Piha—W. A. Beveridge, Rangitoto—J. Carnahan, Narrow Neck—U. V. Dellow, Russell—parties of advanced students.

species are permanently submerged, shaded by the overhanging rock of the pool sides and sheltered by the large algae attached above them. However, algae of the rock pools other than the smaller species are apt to become stunted; especially is this the case in pools of the upper littoral where there is great diversity in the temperature, salinity and aeration of the water. Although these factors, especially salinity, may vary considerably, it is probable that the drying up of the higher pools during neap tide periods is the most important factor. Stagnant pools in the highest littoral are generally inhabited only by green and blue-green algae, and then often to no great extent.

It is advisable, and most interesting, to make a special study of the epiphytes to be found attached to the larger seaweeds inhabiting the pools. Indeed, some epiphytic plants are to be found only in this habitat. Many of the more recent additions to the flora have been epiphytes and no doubt more remain to be found.

CAVES

The algal vegetation of caves has scarcely been studied in New Zealand,[1] but it will be found to possess its own characteristics. The green and brown algae disappear quite close to the entrance, but certain red and blue-green species will penetrate to a considerable distance. Among the red algae it is primarily *Rhodochorton* and encrusting forms (*Petrocelis*, *Hildenbrandtia*, etc.) that are to be found. Several interesting members of the Myxophyceae will also occur if the walls and roof are kept moist by percolating water.

MIGRATION AND SEASONAL CHANGE

The majority of the larger algae, both red and brown, are perennial; that is they survive more than one season. The smaller algae and many of the green algae are annuals and frequently only occur during a brief season. Examples are *Ulothrix* and *Monostroma* spp. which are confined to the spring months and the brown alga *Splachnidium* which, around Auckland, is confined to the period from December to May.[2] As a result of this the shore, so far as subsidiary species are concerned, presents an ever-changing face, and the investigator cannot be satisfied with a single visit to any locality. Some species disappear for periods of varying length: some reappear at the same season each year, others fail for several years and suddenly reappear in great profusion. It is possible that some species migrate vertically as the seasons change, so that one may start the year at a certain level and subsequent crops develop lower down. This problem of migration, together with that of life duration, are both aspects that have hardly been studied in New Zealand.

ENVIRONMENT

There are a number of factors which determine the position that the dominant species occupy on the shore, and which also probably play a part in determining the nature of the plant thallus. The most significant of the environmental factors is the tide, and it is evident that this will bring about variations in conditions from low-water mark right up to high-water mark. The most important feature is that of exposure, which will range from very short periods near low-water mark of spring tides to long periods at high-water mark. During the exposure periods the various algae will lose water, the metabolic processes will be disturbed, changes will occur in the concentration of the sap, and the thallus may be exposed to considerable temperature variations. In the majority of cases we do not know which of these subsidiary effects is most important, but it is likely that different species are affected differently.

Apart from the exposure between successive tides there is also the continuous exposure, which occurs at the higher levels during neap tide periods, when certain algae may be uncovered for several days at a time. This factor is probably a very important one but at present is little understood. Its operation upon delicate thalli, reproduction and establishment of sporelings may be profound.

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[1] A paper by Dellow and Cassie (1955) has just appeared.

[2] Although farther south it has a much longer season or may even be found throughout the year.

The operation of the tidal factor and its subsidiary effects is ultimately seen in the establishment of certain critical levels on the shore, where the change of factors is such that a number of species either reach their upper or lower limit. A certain amount of work on this problem has been carried out in New Zealand[1] at Piha, Rangitoto, Narrow Neck and Russell where it has been found that critical levels exist at mean high-water spring tides, between extreme (lowest) high-water neap tides and mean high-water neap tides, at mean low-water neap tides and mean low-water spring tides.

Apart from the tidal factor there are a number of other factors. At high levels there is the effect of rain in changing the salinity, whilst an outflow of fresh water has a profound effect, bringing about a local development of *Enteromorpha* and blue-green species. The nature and configuration of the rock are important, operating mainly as presence or absence factors for certain species, whereas the tide acts as a primary controlling factor. Strong surf is essential for some species, e.g. presence of *Durvillea*, *Pachymenia*, whilst it eliminates others, e.g. *Carpophyllum* spp.

Light also is a significant factor which operates primarily at high tide when the plants are covered by the maximum amount of water. Sea water readily absorbs light and hence the amount available for photosynthesis diminishes rapidly with depth. It is probably for this reason that the red and brown seaweeds are most commonly found at the lower depth, because the colour of their pigments is a physical or physiological aid to the utilization of the diminished light supply.

Shade as a factor has already been mentioned (p. 7), and it has recently been shown (Ambler & Chapman, 1950) that conditions in a shaded rock pool are very different, especially for temperature, from those in an exposed pool.

The above can be regarded as the principal factors, although there will be local factors operating in nearly every locality, e.g. mud or sand deposition over the rocks, steepness of shore, etc.

DISTRIBUTION

Members of the Myxophyceae found in New Zealand nearly all have a wide distribution outside of the Dominion. Within the country insufficient collecting makes it impossible to consider internal distribution. There is only one endemic species (*Tolypothrix irregularis*, p. 365) and it is extremely doubtful whether this plant exists, or if it does, whether it is fundamentally different from another species of the same genus. The Myophyceae are a primitive group, and since the species are extremely tolerant of conditions the New Zealand representatives can be expected to be fairly widespread.

In the Chlorophyceae the various species and forms are distributed within New Zealand and the associated islands as follows:

General	80	Stewart Island and Sub-antarctic islands	17
North Island	63	Chatham Island	2
Wellington and South Island	41	Kermadec islands	2

Thirty-nine per cent of the total are generally distributed within the Dominion, 31 % are confined to the North Island and 20 % to the South Island. It is interesting to note that there is very little endemism so far as the associated islands are concerned, the sub-antarctic group alone having any considerable number. The two species found only in the Kermadecs and not elsewhere in the New Zealand region are *Caulerpa racemosa*, a tropical species, and *Cladophora fusca*. The two examples from Chatham Island are the local forms of *Chaetomorpha darwinii* and *Bryopsis vestita*.

No less than four of the seventeen species listed in the sub-antarctic group belong to the new genus *Gemina*, which is thus clearly marked as a southern cold-water genus. Within the other three groups there are a number of interesting points. Thus in the South

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[1] Full data are contained in theses by Beveridge, Carnahan and Dellow in Auckland University College library.

Island group *Bryopsis* is the most important genus with ten species (a third of the total) restricted to the area. In fact the South Island appears to have promoted a burst of evolution within the genus.

The North Island group is characterized by possessing seven species of *Monostroma*, many of which are only recorded from the Bay of Islands as a result of the intensive work of Mr V. W. Lindauer. It is, however, likely that these species are more widely distributed, certainly within the North Island. The warm water *Microdictyon mutabilis* is restricted to the North Island, as are also the species of *Prasiola*, though one at least of these (*P. antarctica*) should occur in the South Island. The epiphytic Chaetophorales seem to occur primarily in the North Island, though this may be more apparent than real due to inadequate collecting of such forms. Three species of both *Rhizoclonium* and *Vaucheria* are so far recorded only for the North Island, though this again may be due to lack of collections.

In the general group two-fifths (28) belong to the genus *Enteromorpha* whilst one-fifth is composed of species of *Ulva*. The remaining widely distributed genus is *Chaetomorpha* (seven species), though there are also six species of *Bryopsis* and four of *Rhizoclonium*.

On the whole, the distribution of the Chlorophyceae is not of very great interest, as compared with that of the Phaeophyceae or Rhodophyceae. The most interesting features are provided by the distribution of the species of *Gemina*, *Bryopsis*, *Monostroma* and the members of the Chaetophorales.

Finally, of the total number of Chlorophyceae recorded (205), no less than 92 (47 %) are endemic. This proportion will probably prove not to be so high as it is in the red and brown algae; this may be anticipated because the Chlorophyceae are generally more tolerant of environmental conditions.

For the benefit of those who are interested, the location of the various collecting stations mentioned is given in Table 2. In this table the position of the stations in relation to the marine algal provinces of New Zealand as recognized by Miss L. B. Moore is also listed. I am grateful to Miss Moore for providing most of the material for this table.

TABLE 2. *Localities mentioned in Part I*

		Marine algal province									
				Intermediate		Central					
Locality	District	Kermadec	Auckland	West	East	Wgtn	West S.I.	East S.I.	Forsterian	Chatham	Rossian
Ahaura Bay	East Cape District	—	—	—	E*	—	—	—	—	—	—
Ahuriri Lagoon	Napier	—	—	—	E	—	—	—	—	—	—
Akaroa	Banks Peninsula	—	—	—	—	—	—	E	—	—	—
Akatore	Otago	—	—	—	—	—	—	—	E	—	—
Akitio	Southern Hawke's Bay	—	—	—	E	—	—	—	—	—	—
Allan's Beach	Pihama, Taranaki	—	—	W	—	—	—	—	—	—	—
Anatori River	Nelson	—	—	—	—	—	W	—	—	—	—
Anawhata	Auckland West Coast	—	W	—	—	—	—	—	—	—	—
Aohanga	Wairarapa Coast east of Pongaroa	—	—	—	E	—	—	—	—	—	—
Aorere Bay	Nelson	—	—	—	—	—	W	—	—	—	—
Auckland	—	—	E	—	—	—	—	—	—	—	—
Auckland Is.	—	—	—	—	—	—	—	—	—	—	X
Beacon Rock	Kawhia, Te Maika	—	W	—	—	—	—	—	—	—	—
Beeman	Campbell Is.	—	—	—	—	—	—	—	—	—	X

* E = east coast, W = west coast, X = islands, or Wellington area.

TABLE 2 (cont.)

Locality	District	Marine algal province									
				Intermediate		Central					
		Kermadec	Auckland	West	East	Wgtn	West S.I.	East S.I.	Forsterian	Chatham	Rossian
Bethell's Beach	Auckland West Coast	—	W	—	—	—	—	—	—	—	—
Big Bay	Fiordland	—	—	—	—	—	—	—	W	—	—
Birkdale	Auckland	—	E	—	—	—	—	—	—	—	—
Blackhead (W.A.S.)*	Dunedin	—	—	—	—	—	—	—	E	—	—
Blowholes	Punakaiki, Greymouth	—	—	—	—	—	W	—	—	—	—
Bluff	90 Mile Beach	—	W	—	—	—	—	—	—	—	—
Bluff	Southland	—	—	—	—	—	—	—	E	—	—
The Bluff	Southland	—	—	—	—	—	—	—	E	—	—
Bluff Hill	Southland	—	—	—	—	—	—	—	E	—	—
Breaker Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Brick Bay	Russell	—	E	—	—	—	—	—	—	—	—
Brighton	Otago	—	—	—	—	—	—	—	E	—	—
Bruce Bay	South Westland	—	—	—	—	—	—	—	W	—	—
Buffalo Beach	Coromandel	—	E	—	—	—	—	—	—	—	—
Butterfields Beach	Stewart Is.	—	—	—	—	—	—	—	E	—	—
Campbell Bay	Auckland	—	E	—	—	—	—	—	—	—	—
Campbell's Beach	Pihama	—	—	W	—	—	—	—	—	—	—
Canoe Creek	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Cape Brett	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Cape Campbell	Marlborough	—	—	—	—	—	—	E	—	—	—
Cape Egmont	Taranaki	—	—	W	—	—	—	—	—	—	—
Cape Foulwind	Westport	—	—	—	—	—	W	—	—	—	—
Cape Maria van Diemen	Bay of Plenty	—	W	—	—	—	—	—	—	—	—
Cape Runaway	Wairarapa	—	E	—	—	—	—	—	—	—	—
Cape Turakirae	Between Port Nicholson and Palliser Bay	—	—	—	—	X	—	—	—	—	—
Cape Turnagain	—	—	—	—	E	—	—	—	—	—	—
Castle Point	Wairarapa	—	—	—	—	X	—	—	—	—	—
Caswell Sound	Fiordland	—	—	—	—	—	—	—	W	—	—
Catharine Bay	Great Barrier Is.	—	E	—	—	—	—	—	—	—	—
Catlins	Otago	—	—	—	—	—	—	—	E	—	—
Cave Rock	Sumner	—	—	—	—	—	—	E	—	—	—
Chalky Is.	Chalky Inlet	—	—	—	—	—	—	—	W	—	—
Charteris Bay	Bank's Peninsula	—	—	—	—	—	—	E	—	—	—
Collingwood River, Aorere	N.W. Nelson	—	—	—	—	—	W	—	—	—	—
Coromandel	—	—	E	—	—	—	—	—	—	—	—
Cunning Cove	—	—	—	—	—	—	—	—	W	—	—
Deep Cove	Doubtful Sound	—	—	—	—	—	—	—	W	—	—
Deepwater Cove	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Diamond Harbour	Lyttelton	—	—	—	—	—	—	E	—	—	—
Dillon R.	Pelorous Sound	—	—	—	—	—	—	E	—	—	—
Doubtful Sound	—	—	—	—	—	—	—	—	W	—	—
D'Urville Is.	Nelson	—	—	—	—	—	W	—	—	—	—
Dusky Sound	—	—	—	—	—	—	—	—	W	—	—
Emergency Bay	Carnley Harbour, Auckland Is.	—	—	—	—	—	—	—	—	—	X
Evans Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Fanal Is. (Mokoninau Is.)	Hauraki Gulf	—	E	—	—	—	—	—	—	—	—
Fifeshore Rock	Nelson	—	—	—	—	—	W	—	—	—	—
Fishing Rock	Raoul Il. Kermadec Is.	X	—	—	—	—	—	—	—	—	—
Fox R.	Westland	—	—	—	—	—	W	—	—	—	—
Foxton	Manawatu	—	—	W	—	—	—	—	—	—	—
Frenchman's Creek	Russell	—	E	—	—	—	—	—	—	—	—

* W. A. Setchell, who identified much of Laing's material.

TABLE 2 (cont.)

		Marine algal province									
				Intermediate		Central					
Locality	District	Kermadec	Auckland	West	East	Wgtn	West S.I.	East S.I.	Forsterian	Chatham	Rossian
Gannet Rocks	Hauraki Gulf	—	E	—	—	—	—	—	—	—	—
George Sound	Southern Fiords	—	—	—	—	—	—	—	W	—	—
Gisborne	—	—	—	—	E	—	—	—	—	—	—
Gladstone Pier	Lyttelton	—	—	—	—	—	—	E	—	—	—
Goose Bay	Kaikoura	—	—	—	—	—	—	E	—	—	—
Gore Bay	North Canterbury	—	—	—	—	—	—	E	—	—	—
Grassmere lagoon	Blenheim	—	—	—	—	—	—	E	—	—	—
Great Island	Chalky Inlet	—	—	—	—	—	—	—	W	—	—
Green Is. Lagoon	Dunedin	—	—	—	—	—	—	—	E	—	—
Green Is.	Dunedin	—	—	—	—	—	—	—	E	—	—
Greymouth	—	—	—	—	—	—	W	—	—	—	—
Half Moon Bay	Stewart Is.	—	—	—	—	—	—	—	E	—	—
Hampden	North Otago	—	—	—	—	—	—	—	E	—	—
Happy Valley	Wellington	—	—	—	—	X	—	—	—	—	—
Haulashore Cove	Dusky Sound	—	—	—	—	—	—	—	W	—	—
Havelock	Marlborough Sound	—	—	—	—	—	—	E	—	—	—
Hawke's Bay	—	—	—	—	E	—	—	—	—	—	—
Heaphy River	S.W. Nelson	—	—	—	—	—	W	—	—	—	—
Helensville	S. Kaipara	—	W	—	—	—	—	—	—	—	—
Hen and Chicken Is.	Auckland	—	E	—	—	—	—	—	—	—	—
Hicks Bay	East Cape	—	—	—	E	—	—	—	—	—	—
Hobson's Bay	Auckland	—	E	—	—	—	—	—	—	—	—
Hohura	North Auckland	—	E	—	—	—	—	—	—	—	—
Hokianga Heads	—	—	W	—	—	—	—	—	—	—	—
Hokio Beach	Levin	—	—	W	—	—	—	—	—	—	—
Hokitika	—	—	—	—	—	—	W	—	—	—	—
Honga Point	South of Lyall Bay, Wellington	—	—	—	—	X	—	—	—	—	—
Hooper's Inlet	Otago Peninsula	—	—	—	—	—	—	—	E	—	—
Horoera	East Cape District	—	—	—	E	—	—	—	—	—	—
Horseshoe Bay	East Cape	—	—	—	E	—	—	—	—	—	—
Houghton Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Howick	Auckland	—	E	—	—	—	—	—	—	—	—
Island Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Islington Bay	Rangitoto	—	E	—	—	—	—	—	—	—	—
Jacks Bay	Catlins, Southland	—	—	—	—	—	—	—	E	—	—
Julians Beach	Pihama	—	—	W	—	—	—	—	—	—	—
Kaikorai Stream	Dunedin	—	—	—	—	—	—	—	E	—	—
Kaikoura	—	—	—	—	—	—	—	E	—	—	—
Karaka Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Karamea	N.W. Nelson	—	—	—	—	—	W	—	—	—	—
Karetane	Otago	—	—	—	—	—	—	—	E	—	—
Karihana Bay	Plimmerton	—	—	—	—	X	—	—	—	—	—
South Karori Stream	North Shore, Cook Str.	—	—	—	—	X	—	—	—	—	—
Kartigi	Otago	—	—	—	—	—	—	—	E	—	—
Kena Beach*	—	—	—	—	—	—	—	—	—	—	—
Keri Keri	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Keyhole Rock	Anawhata, Auckland West Coast	—	W	—	—	—	—	—	—	—	—
Kokorua Beach	—	—	—	—	—	—	W	—	—	—	—
Konga Bay	South of Lyall Bay, Wellington	—	—	—	—	X	—	—	—	—	—
Kowhaihai R.	W. Nelson	—	—	—	—	—	W	—	—	—	—

* Localities not placed in a province are recorded on herbarium sheets but cannot be traced on maps.

TABLE 2 (cont.)

		Marine algal province									
				Intermediate		Central					
Locality	District	Kermadec	Auckland	West	East	Wgtn	West S.I.	East S.I.	Forsterian	Chatham	Russian
Kuri Bush	Dunedin	—	—	—	—	—	—	—	E	—	—
Lake Ellesmere	Canterbury	—	—	—	—	—	—	E	—	—	—
Lake Forsyth	Banks Peninsula	—	—	—	—	—	—	E	—	—	—
Lawyers Head	Dunedin	—	—	—	—	—	—	—	E	—	—
Leigh	Auckland	—	E	—	—	—	—	—	—	—	—
Levin	Manawatu	—	—	W	—	—	—	—	—	—	—
Lion Rock	Piha, Auckland West Coast	—	W	—	—	—	—	—	—	—	—
Little Barrier Is.	Hauraki Gulf	—	E	—	—	—	—	—	—	—	—
Little Wanganui River	N.W. Nelson	—	—	—	—	—	W	—	—	—	—
Long Beach	Russell	—	E	—	—	—	—	—	—	—	—
Long Beach (W.A.S. 1917)	Otago	—	—	—	—	—	—	—	E	—	—
Long Is.	Dusky Sound	—	—	—	—	—	—	—	W	—	—
Lowry Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Lyall Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Lyttelton	—	—	—	—	—	—	—	E	—	—	—
MacAndrew Bay	Otago	—	—	—	—	—	—	—	E	—	—
Mahia Peninsula	Hawke's Bay	—	—	—	E	—	—	—	—	—	—
Mairangi Beach	(Nr. Campbell Bay) Auckland	—	E	—	—	—	—	—	—	—	—
Makara Beach	Wellington	—	—	—	—	X	—	—	—	—	—
Maketu	Bay of Plenty	—	E	—	—	—	—	—	—	—	—
Manakau	Auckland	—	W	—	—	—	—	—	—	—	—
Mansion House Bay	Kawau Is.	—	E	—	—	—	—	—	—	—	—
Maranui Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Mataikona R.	N. of Castlepoint	—	—	—	E	—	—	—	—	—	—
Matakana Heads	Hauraki Gulf (opp. Kawau)	—	E	—	—	—	—	—	—	—	—
Matarangi Beach	Kuaotunu, Mercury Bay	—	E	—	—	—	—	—	—	—	—
Matauhi Bay	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Matauri Bay	Whangaroa County	—	E	—	—	—	—	—	—	—	—
Mercury Bay	Coromandel	—	E	—	—	—	—	—	—	—	—
Micks Creek	Warkworth	—	E	—	—	—	—	—	—	—	—
Mikotahi	New Plymouth	—	—	W	—	—	—	—	—	—	—
Mitimiti	Hokianga	—	W	—	—	—	—	—	—	—	—
Moa Pt.	Wellington	—	—	—	—	X	—	—	—	—	—
Moeraki	North Otago	—	—	—	—	—	—	—	E	—	—
Moeraki (Lighthouse)	Otago	—	—	—	—	—	—	—	E	—	—
Mokohinau Is.	Hauraki Gulf	—	E	—	—	—	—	—	—	—	—
Mossy Creek	Karamea	—	—	—	—	—	W	—	—	—	—
Moto Arohia	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Moturoa	Russell	—	E	—	—	—	—	—	—	—	—
Motutapu	Auckland	—	E	—	—	—	—	—	—	—	—
Mt. Manganoui	Bay of Plenty	—	—	—	E	—	—	—	—	—	—
Napier	Hawke's Bay	—	—	—	E	—	—	—	—	—	—
Narrow Neck	Auckland	—	E	—	—	—	—	—	—	—	—
Native Is. (= Rabbit Is.)	Paterson Inlet, Stewart Is.	—	—	—	—	—	—	—	E	—	—
Nelson	—	—	—	—	—	—	X	—	—	—	—
N. Caroline Bay	Timaru	—	—	—	—	—	—	—	E	—	—
North Heads (W.A.S. 1917)	Otago Harbour	—	—	—	—	—	—	—	E	—	
90 Mile Beach	North Auckland	—	W	—	—	—	—	—	—	—	—
Oahoa*	—	—	—	—	—	—	—	—	—	—	—

TABLE 2 (cont.)

		Marine algal province									
				Intermediate		Central					
Locality	District	Kermadec	Auckland	West	East	Wgtn	West S.I.	East S.I.	Forsterian	Chatham	Rossian
Oaro	Kaikoura Coast	—	—	—	—	—	—	E	—	—	—
Ocean Beach	Cape Kidnappers	—	—	—	E	—	—	—	—	—	—
Oeo Beach	Pihama	—	—	W	—	—	—	—	—	—	—
Ohau Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Ohiro Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Old Camp Site	White Is.	—	E	—	—	—	—	—	—	—	—
O'Neill's Beach	Auckland West Coast	—	W	—	—	—	—	—	—	—	—
Onewhero	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Opunake	Taranaki	—	—	W	—	—	—	—	—	—	—
Orewa	Auckland	—	E	—	—	—	—	—	—	—	—
Orongo Bay	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Otago Harbour	—	—	—	—	—	—	—	—	E	—	—
Otehei Bay	Urupukapuka Is., Bay of Islands	—	E	—	—	—	—	—	—	—	—
Otipua Lagoon	Timaru	—	—	—	—	—	—	—	E	—	—
Otu Bay	D'Urville Is. W.	—	—	—	—	—	W	—	—	—	—
Otumoetai Beach	Tauranga	—	E	—	—	—	—	—	—	—	—
Owenga	Chatham Is.	—	—	—	—	—	—	—	—	X	—
Parakino Bridge	Wanganui	—	—	W	—	—	—	—	—	—	—
Parapara R.	N.W. Nelson	—	—	—	—	—	W	—	—	—	—
Paremata	Porirua Harbour, Wgtn	—	—	—	—	X	—	—	—	—	—
Pareoa	Greymouth	—	—	—	—	—	W	—	—	—	—
Parnell	Auckland	—	E	—	—	—	—	—	—	—	—
Parrot Is.	Dusky Sound	—	—	—	—	—	—	—	W	—	—
Parua Bay	Whangarei	—	E	—	—	—	—	—	—	—	—
Patarau North = north of river mouth	N.W. Nelson, west coast	—	—	—	—	—	W	—	—	—	—
Patea	Taranaki	—	—	W	—	—	—	—	—	—	—
Paterson's Inlet	Stewart Is.	—	—	—	—	—	—	—	E	—	—
Patiti Pt.	Timaru	—	—	—	—	—	—	—	E	—	—
Pegasus	Stewart Is.	—	—	—	—	—	—	—	X	—	—
Pencarrow Head	Cook Strait	—	—	—	—	X	—	—	—	—	—
Penguin Harbour	Campbell Is.	—	—	—	—	—	—	—	—	—	X
Perpendicular Pt.	Greymouth, Westland	—	—	—	—	—	W	—	—	—	—
Petone	Wellington	—	—	—	—	X	—	—	—	—	—
Picton	Marlborough	—	—	—	—	—	—	E	—	—	—
Piha	Auckland	—	W	—	—	—	—	—	—	—	—
Pihama	Taranaki, south coast	—	—	W	—	—	—	—	—	—	—
Pile Bay	Lyttelton	—	—	—	—	—	—	E	—	—	—
Pinnacles	Little Barrier Is.	—	E	—	—	—	—	—	—	—	—
Point Elizabeth	Westland	—	—	—	—	—	—	—	W	—	—
Poor Knights	N. Auckland	—	E	—	—	—	—	—	—	—	—
Porangahau	Southern Hawkes Bay	—	—	—	E	—	—	—	—	—	—
Port Adventure	Stewart Is.	—	—	—	—	—	—	—	E	—	—
Port Chalmers	Otago Harbour	—	—	—	—	—	—	—	E	—	—
Pt. de la Vive	Campbell Is.	—	—	—	—	—	—	—	—	—	X
Port Elizabeth*	—	—	—	—	—	—	—	—	—	—	—
Port Howard	Wellington Harbour	—	—	—	—	X	—	—	—	—	—
Port Nicholson	Wellington	—	—	—	—	X	—	—	—	—	—
Port Nelson	—	—	—	—	—	—	W	—	—	—	—
Port William	Stewart Is.	—	—	—	—	—	—	—	X	—	—
Portobello	Otago Harbour	—	—	—	—	—	—	—	E	—	—
Poverty Bay	Gisborne	—	—	—	E	—	—	—	—	—	—
Princess Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Puketeraki	Otago	—	—	—	—	—	—	—	E	—	—

TABLE 2 (cont.)

		Marine algal province									
				Intermediate		Central					
Locality	District	Kermadec	Auckland	West	East	Wgtn	West S.I.	East S.I.	Forsterian	Chatham	Rossian
Punakaiki	Greymouth	—	—	—	—	—	W	—	—	—	—
Punipaua Rocks	Patarau, N. W. Nelson	—	—	—	—	—	W	—	—	—	—
Puponga Stream	Collingwood, N.W. Nelson	—	—	—	—	—	W	—	—	—	—
Purakanui	Otago	—	—	—	—	—	—	—	E	—	—
Queen Charlotte Sd.	Marlborough	—	—	—	—	—	—	E	—	—	—
Rabbit Is. (syn. Native Is.)	Paterson Inlet, Stewart Is.	—	—	—	—	—	—	—	E	—	—
Rangiahuia Bay	Hokianga	—	W	—	—	—	—	—	—	—	—
Rangiputa	North Auckland	—	E	—	—	—	—	—	—	—	—
Rangitoto	Auckland	—	E	—	—	—	—	—	—	—	—
Rangitoto Channel	Auckland	—	E	—	—	—	—	—	—	—	—
Reef Pt.	North Auckland	—	W	—	—	—	—	—	—	—	—
Riverton	Southland	—	—	—	—	—	—	—	E	—	—
Riverton Pt.	Southland	—	—	—	—	—	—	—	E	—	—
Robinson's Bay	Banks Peninsula	—	—	—	—	—	—	E	—	—	—
Rosebank	Auckland (Waitemata)	—	E	—	—	—	—	—	—	—	—
Ruby Bay	Nelson	—	—	—	—	—	W	—	—	—	—
Run-around	Wellington	—	—	—	—	X	—	—	—	—	—
Russell	Bay of Islands	—	E	—	—	—	—	—	—	—	—
St Clair	Dunedin	—	—	—	—	—	—	—	E	—	—
Scorching Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Scotts Point	90 Mile Beach	—	W	—	—	—	—	—	—	—	—
Seal Pt. Rocks	Otago Peninsula	—	—	—	—	—	—	—	E	—	—
Seatoun	Wellington	—	—	—	—	X	—	—	—	—	—
Seaview (W.A.S.)	Otago	—	—	—	—	—	—	—	E	—	—
Shag Pt.	Otago	—	—	—	—	—	—	—	E	—	—
Ship Cove	Queen Charlotte Sound	—	—	—	—	—	—	E	—	—	—
Shoal Pt.	Campbell Is.	—	—	—	—	—	—	—	—	—	X
Sinclair Head	Cook Straight N.I.	—	—	—	—	X	—	—	—	—	—
Smoothwater Bay	Campbell Is.	—	—	—	—	—	—	—	—	—	X
Snares Is.	—	—	—	—	—	—	—	—	W	—	—
Stanmore Bay	Whangaparaoa Peninsula	—	E	—	—	—	—	—	—	—	—
Stewart Is.	—	—	—	—	—	—	—	—	X	—	—
Sumner	Christchurch	—	—	—	—	—	—	E	—	—	—
Table Cape	Mahia Peninsula	—	—	—	E	—	—	—	—	—	—
Tahuna	Nelson	—	—	—	—	—	W	—	—	—	—
Tahunanui Bay	Nelson	—	—	—	—	—	W	—	—	—	—
Taieri Beach	Otago	—	—	—	—	—	—	—	E	—	—
Tairua Heads	Coromandel	—	E	—	—	—	—	—	—	—	—
Taranga Is.	Auckland	—	E	—	—	—	—	—	—	—	—
Tauranga	Bay of Plenty	—	E	—	—	—	—	—	—	—	—
Tauranga Bay	C. Foulwind, Westland	—	—	—	—	—	W	—	—	—	—
Tautuku Bay	Catlins District	—	—	—	—	—	—	—	E	—	—
Taylor's Mistake	Banks Peninsula	—	—	—	—	—	—	E	—	—	—
Te Araroa	East Cape	—	—	—	E	—	—	—	—	—	—
Te Kaha	Bay of Plenty	—	E	—	—	—	—	—	—	—	—
Te Kaminaru Bay	W. Wellington	—	—	—	—	X	—	—	—	—	—
Te Mahia	Kenepuru Sound, Marlborough	—	—	—	—	—	—	E	—	—	—
Te Maika	Kawhia	—	W	—	—	—	—	—	—	—	—
Te Oka, Little River	Canterbury	—	—	—	—	—	—	E	—	—	—
Te Oka,	Little River, South of Banks Peninsula	—	—	—	—	—	—	E	—	—	—
Te One	Chatham Island	—	—	—	—	—	—	—	—	X	—
Te Papa*	—	—	—	—	—	—	—	—	—	—	—

Table 2 (cont.)

		Marine algal province									
				Intermediate		Central					
Locality	District	Kermadec	Auckland	West	East	Wgtn	West S.I.	East S.I.	Forsterian	Chatham	Rossian
Thames	—	—	E	—	—	—	—	—	—	—	—
Thornton's Bay	Thames	—	E	—	—	—	—	—	—	—	—
Timaru	—	—	—	—	—	—	—	—	E	—	—
Tinopai	Kaipara	—	W	—	—	—	—	—	—	—	—
Titahi Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Tokomaru Bay	East Cape District	—	—	—	E	—	—	—	—	—	—
Tongue Point	Cook Str. N.I.	—	—	—	—	X	—	—	—	—	—
Tucker Cove	Campbell Is.	—	—	—	—	—	—	—	—	—	X
Tunnel Beach (W.S.A.)	Otago	—	—	—	—	—	—	—	E	—	—
12 Mile Beach	Greymouth	—	—	—	—	—	W	—	—	—	—
Uruiti	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Waihau Bay	Bay of Plenty	—	E	—	—	—	—	—	—	—	—
Waihi	Bay of Plenty	—	E	—	—	—	—	—	—	—	—
Waikanae Salt Marsh	Wellington W.C.	—	—	—	—	X	—	—	—	—	—
Lr. Waikareao Arm	Tauranga	—	E	—	—	—	—	—	—	—	—
Waikouaiti	Dunedin	—	—	—	—	—	—	E	—	—	—
Waimakerere	Christchurch	—	—	—	—	—	—	E	—	—	—
Waimamaku	South of Hokianga	—	W	—	—	—	—	—	—	—	—
Wainui Bay	Whangaroa	—	E	—	—	—	—	—	—	—	—
Waipapa	Christchurch	—	—	—	—	—	—	E	—	—	—
Waipawa	Little Barrier Is.	—	E	—	—	—	—	—	—	—	—
Waitaki	Timaru	—	—	—	—	—	—	—	E	—	—
Waitangi	Chatham Is.	—	—	—	—	—	—	—	—	X	—
Waitangi	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Waitara	New Plymouth	—	—	W	—	—	—	—	—	—	—
Waitata	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Waiuku Rd.	Auckland	—	W	—	—	—	—	—	—	—	—
Waiwera	Auckland	—	E	—	—	—	—	—	—	—	—
Wardell's Creek	Bay of Islands	—	E	—	—	—	—	—	—	—	—
Warkworth	Auckland	—	E	—	—	—	—	—	—	—	—
Warrington	Otago	—	—	—	—	—	—	—	E	—	—
Wellington	—	—	—	—	—	X	—	—	—	—	—
West Head	Wellington	—	—	—	—	X	—	—	—	—	—
West Pt.	White Island	—	E	—	—	—	—	—	—	—	—
Whakataki	Wairarapa E. Coast	—	—	—	E	—	—	—	—	—	—
Whale Bay	Raglan	—	W	—	—	—	—	—	—	—	—
Whangape	North Hokianga	—	W	—	—	—	—	—	—	—	—
Whangarei	—	—	E	—	—	—	—	—	—	—	—
Whareatea R.	North of Westport	—	—	—	—	—	W	—	—	—	—
Whareponga	East of Ruatoria	—	—	—	E	—	—	—	—	—	—
White Island	Bay of Plenty	—	—	—	E	—	—	—	—	—	—
Windlass Bay	West Coast, Campbell Is.	—	—	—	—	—	—	—	—	—	W
Worser Bay	Wellington	—	—	—	—	X	—	—	—	—	—
Wycliffe Bay	Dunedin	—	—	—	—	—	—	—	E	—	—

Note. Since the list was first compiled a number of records have come to hand (Dellow, Ph.D. Thesis, Auckland University College) from the Hauraki Gulf. Records were made at Te Puru, Raukura Pt. (Firth of Thames), St Heliers, Arkles Bay (Auckland), Te Haruhi Bay, Whangaparaoa Heads, Cape Rodney, Kawau Is. (North of Auckland), Noises Is., Shag Rock, Waiheke Is. (Surfdale, Arran, Anita Bay, Palm Beach, Oneroa), Little Barrier Is. (Hauturu, Ti Titoki, Pohutakawa Flat), Coromandel Peninsula (Long Beach, Fletcher's Bay, Sugar Loaf Rocks, Whitianga Bay), Great Barrier Is. (Whangaparapara, Port Fitzroy, Needle Point, Oruawharo Bay).

Further records have been published by Chapman from the Three Kings Islands, by Naylor for Dunedin with the additional localities of Allen Beach and the Kaik, and I have also had records from G. A. Knox of Canterbury University College for Godley Head and Colne Bay of the Banks Peninsula.

MYXOPHYCEAE

The plants in this class are characterized by the blue-green colour of the pigment, primarily caused by the substance phycocyanin. The plant body ranges from a single cell to colonial forms (the individual cells often embedded in a gelatinous matrix) and multicellular plants. In the colonial forms there may be distinct individual sheaths, or the sheaths may become homogeneous with the matrix. The great majority of the multicellular plants are filamentous, with or without sheaths. One family (Pleurocapsaceae) has both erect and prostrate filaments and therefore exhibits heterotrichy. The remaining filamentous forms are divided into those that possess special bodies known as heterocysts and those that do not have heterocysts (Oscillatoriaceae). Filamentous forms can also exhibit true or false branching in which there is a break between the axis and the branch. There is no true nucleus, and reproduction is of the simplest kind, primarily vegetative, or else by special portions known as hormogones (in the filamentous forms) or by non-motile gonidia (non-filamentous forms). There is no sexual reproduction.

Up to the present time, the marine members of this class have not been studied very closely in New Zealand. Only a small number were recorded by Laing (1926). The present list is moderately extensive, but many more records are required and no doubt more species will be added. The distribution of the recorded species is undoubtedly much wider than appears, and future workers should add new localities.

In preparing this list I am particularly grateful to Dr Francis Drouet, of the Chicago Natural History Museum, who has determined the great majority of the specimens.

The members of the Myxophyceae are very widespread, and the only species with restricted distribution are found in the genus *Rivularia*.

The arrangement of the families and orders follows that given in Fritsch (1945). All New Zealand references available to the author have been cited for each species: apart from these, one or two additional references are added, either to the original description or to some other good description.

KEY TO THE FAMILIES IN NEW ZEALAND

1. Unicellular, multiplication by fission. 2
   Filamentous, multiplication by hormogones. 3
2. Cells showing a difference between basal and apical region, reproduction by gonidia. Chamaesiphonaceae
   Cells not differentiated into basal and apical region, reproduction by vegetative division. Chroococcaceae
3. Heterocysts absent. Oscillatoriaceae
   Heterocysts present. 4
4. Filaments[1] tapering from base to apex. Rivulariaceae
   Filaments not tapering. 5
5. Sheaths delicate, filaments entangled. Nostocaceae
   Sheaths firm, filaments with false branching. Scytonemataceae

CHROOCOCCALES

Unicellular or colonial, often palmelloid, without any polarity; multiplication by cell division and by endospores.

CHROOCOCCACEAE

Plants showing no difference between basal and apical regions; solitary or aggregated into colonies; reproduction by vegetative division.

1. Individual sheaths distinct. 2
   Individual sheaths not distinct. *Anacystis*

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[1] The filament is the algal thread plus the sheath.

2. Cells solitary or in small families. *Chroococcus*
   Many cells in a colony. 3
3. Cells spherical. *Gloeocapsa*
   Cells oval or cylindric. 4
4. Plant mass globose or subglobose. *Coccochloris*
   Plant mass amorphous. *Gloeothece*

Anacystis Menegh.

Plant mass more or less spherical, colourless, blue-green, yellow or brown; individual sheaths indistinct, confluent into a mucous, homogeneous envelope.

Anacystis marina (Hansg.) Dr. & Daily

Newton, *Handb. Brit. Seaw.* p. 3, 1931 as *Aphanocapsa marina* Hansg.

Colony small, green, gelatinous, subglobose; peripheral cells oblong or rarely subglobose, 6–7·5 × 5μ, often in pairs; cell wall delicate. (Fig. 4, no. 11.)

Distribution. Local: Piha, Rangitoto, Hobson's Bay, Russell and probably elsewhere. Mid. to upper littoral. General: cosmopolitan.

This species forms small gelatinous masses caught in the thallus of larger algae.

Gloeothece Naeg.

Colonies embedded in a common gelatinous envelope; cells cylindric-oblong, each surrounded by a wide, mucous, homogeneous or lamellose sheath.

Gloeothece linearis Naeg.

Naegeli, *Gatt. Einz. Alg.* p. 58, 1849.

Plant mass gelatinous, dull yellow, becoming reddish; plants 9·5–10·5μ wide, 10·5–18μ long; sheaths very wide, colourless, hyaline, oblong or somewhat reniform; cells 0·8–2·5μ diam., linear-cylindrical, straight or curved; contents pale blue-green or green. (Fig. 1, no. 2.)

Distribution. Local: cave, Piha. General: Europe, West Indies.

Chroococcus Naeg.

Plants free-floating or forming a gelatinous or crust-like plant mass, occurring as spherical or angular cells, each surrounded by a more or less definite sheath, solitary or united in twos, fours, eights, but not held together in definite colonies by a common gelatinous tegument; sheaths thin or wide, homogeneous or lamellose, colourless or coloured; cell contents homogeneous or granular, usually blue-green, sometimes violet, olive-green, orange or yellowish; reproduction by successive division of the cells alternately in three directions.

(1) *Chroococcus turgidus* (Kütz.) Naeg. var. *maximus* Nygaard.

Chapman, *J. Linn. Soc.* (*Bot.*), **51**, 221, 1937.

Cells usually 2, more rarely 3–4, blue-green, with sheath 67–70μ, without sheath 57–60μ diam.; sheath homogeneous, colourless. (Fig. 2*a*.)

Distribution. Local: Russell, in upper tide pools; lagoon, Grassmere. General: Europe.

This form is very similar in its measurements to *C. giganteus* from which, however, it differs in the non-lamellate character of the sheath.

Gloeocapsa Kütz.

Cells spherical, either single or more commonly a number associated in families; each cell enclosed in a strongly thickened, usually distinctly lamellose sheath, colourless or coloured; cell contents blue-green, bluish, steel-blue, reddish or yellowish; reproduction by division in all planes.

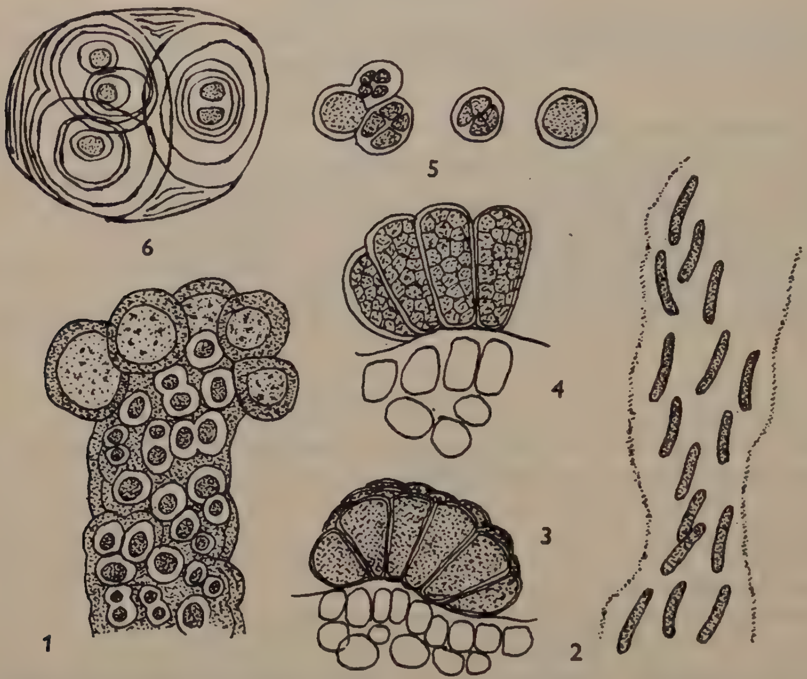

Fig. 1. 1, *Entophysalis deusta*; 2, *Gloeothece linearis*; 3, *Entophysalis conferta*—vegetative; 4, *E. conferta* with gonidia; 5, *E. conferta*—young cells; 6, *Gloeocapsa alpicola*. (All × 500–700.) (1, after Engler and Prantl; 2, after W. & G. S. West; 3, 4, after Bornet and Thuret; 5, after Hauck; 6, after Lemmerman.)

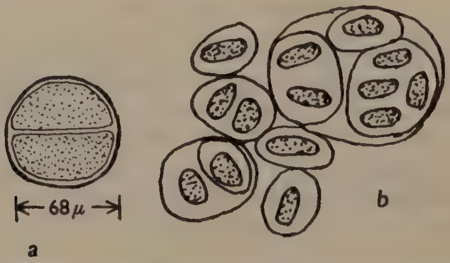

Fig. 2. (*a*) *Chroococcus turgidus* var. *maxima*; (*b*) *Coccochloris stagnina* var. *rupestris*. (× 600.) (*b*, after Cooke.)

Gloeocapsa alpicola (Lyngb.) Born.

Lyngb., *Tent. Hydr. Dan.* p. 206, 1819; Kütz., *Tab. Phyc.* 1, tab. 22, fig. 1, 1845 as *G. magma*.

Plant mass crustaceous, coppery purple, becoming black on drying; cell families 30–70, rarely 300μ dia.; plants 6–12μ dia., spherical; sheaths lamellose, deep purple or copper brown, rarely colourless; outer layer very broad and paler; cells 4·5–7μ dia., spherical. (Fig. 1, no. 6.)

Distribution. Local: mangrove swamp, Russell, Coromandel, Waiwera (on *Lichina* in middle littoral), Waiheke. General: more or less cosmopolitan.

Coccochloris (C. Sprengel) Kirchn.

Cells in a homogeneous gelatinous matrix, globose or subglobose; cells elongate.

Coccochloris stagnina f. *rupestris* (Lyngb.) Dr. & Daily

Tilden, *Minn. Algae*, p. 26, Pl. 2, fig. 4, 1910 (as *Gloeothece rupestris*); Drouet and Daily, *Lloydia*, **11**, 78, 1948.

Colonies 25–45μ dia., spherical or oval, containing 2, 4 or 8 plants; plants 8–12μ dia., 12–36μ long; sheaths colourless or brownish yellow, cells 4–5·5μ dia., 6–15μ long; blue-green. (Fig. 2*b*.)

Distribution. Local: mangrove swamp, Russell and Orewa. General: California, Bermuda, Europe, Faeroes, Azores, Sardinia.

CHAMAESIPHONALES

Unicellular or colonial epiphytes or lithophytes exhibiting marked polarity; multiplication by endospores.

Chamaesiphonaceae

Plants showing a difference between basal and apical regions; solitary or united into colonies, usually epiphytic; reproduction by cell division, fragmentation or by non-mobile gonidia.

The arrangement followed here is that proposed by Drouet & Daily (1948) and it is based upon a study of life histories. There is only the one family in the order.

Entophysalis Kütz.

Plant mass forming cushions or layers, including numerous, more or less confluent, small families of spherical, ovoid or cylindrical cells, each surrounded by an elliptical sheath.

1.	Growing on rock, shells or woodwork.	*E. deusta*
	Growing on other algae.	*E. conferta*

(1) *Entophysalis deusta* (Menegh.) Dr. & Daily

Kütz., *Phyc. Gen.* p. 177, pl. 17, fig. 5, 1843, as *E. granulosa*; Drouet & Daily, *Lloydia*, **11**, 79, 1948.

Plant mass crustaceous, up to 1 mm. thick, granular and warted, brownish or black; cells 2–5μ dia., sheaths very thick, lamellose, brownish. (Fig. 1, no. 1.) V.W.L. 26[1] as *Placoma vesiculosa*. Upper littoral.

Distribution. Local: rocks near H.W.M., Scott's Pt., Bay of Islands, Stanmore Bay, Leigh, Cape Rodney, Fletcher's Bay, Sugar Loaf Rk, Poor Knights, Little Barrier, Great Barrier, Bounty Is., Parua Bay (W.A.S.[2]), Tahunanui Bay. General: Maine, New Jersey, Europe, South Australia.

According to Drouet this species is variable, and plants previously known as *Entophysalis granulosa* and *Placoma vesiculosa* are simply two different growth forms.

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[1] These numbers refer to the exsiccatae of New Zealand algae distributed by V. W. Lindauer.

[2] W. A. Setchell.

(2) *Entophysalis conferta* (Kütz.) Dr. & Daily

Born. & Thur., *Notes Algol.* **2**, 73, pl. 26, figs. 6–9, 1880, as *Dermocarpa prasina*; Drouet, *Lloydia*, **11**, 79, 1948; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 94, 1923, as *Xenococcus schousboei.*

Colony forming an epiphytic cushion-like expansion; cells 4–24μ wide, 15–30μ long, cylindric-oblong, closely packed and laterally compressed; cell contents blue-green or green, later becoming olive or brownish (Fig. 1, nos. 3, 4).

DISTRIBUTION. Local: On *Calothrix crustacea*, *Rhodochorton rothii*, *Rhizoclonium*, Bay of Islands, Orewa, Stanmore, Whangaparaoa, Little Barrier, Fletcher's Bay; on *Centroceras clavulatum*, Narrow Neck; on *Enteromorpha* sp., Piha; on *Lyngbya aestuarii*, Bluff; on *Cladophora* sp., Stewart Is., and probably elsewhere. General: Europe, Alaska, New England.

According to Drouet (personal communication) the growth forms of this species are extremely variable, and it includes all previous records for New Zealand species of *Dermocarpa* and *Xenococcus*.

NOSTOCALES

Non-heterotrichous filaments, often showing false, more rarely true, branching, frequently enclosed in a gelatinous envelope; heterocysts commonly present; multiplication by hormogones, hormocysts and akinetes.

1.	Heterocysts absent.	Oscillatoriaceae
	Heterocysts present.	2
2.	Filaments uniform, unbranched.	Nostocaceae
	Filaments with false branching.	3
3.	Filaments not tapering, false branching by perforation of sheath.	Scytonemataceae
	False branching by development at side.	Rivulariaceae

OSCILLATORIACEAE

Trichomes simple, with or without a sheath; sheaths variable, more or less gelatinous; cells of trichome uniform except for apical cells which may taper or be capitate; reproduction by vegetative division or hormogones.[1]

1.	Sheath absent.	2
	Sheath present.	3
2.	Trichomes straight or nearly so.	*Oscillatoria*
	Trichomes forming a regular spiral.	*Spirulina*
3.	Trichomes single within sheath.	4
	Trichomes several within sheath.	6
4.	Trichomes simple, matted.	5
	Trichomes branched, fasciculate.	*Symploca*
5.	Sheaths thin, hyaline, more or less diffluent, uniting into leathery or papery strata.	*Phormidium*
	Sheaths firm, distinct, not mucous or diffluent, simple or forming a matted mass.	*Lyngbya*
6.	Trichomes few within sheath.	7
	Trichomes many within sheath.	8
7.	Sheath mucous, diffluent, apex of trichome capitate.	*Hydrocoleus*
	Filaments branched, sheath solid, apical cell conical.	*Schizothrix*
8.	Trichomes numerous throughout.	*Microcoleus*
	Trichomes reduced in number in branches.	*Schizothrix*

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[1] Short lengths of trichome separated off for reproduction.

Oscillatoria Vaucher

Trichomes simple, free, mobile, without a sheath or else enclosed within a very thin, fragile, mucous sheath, smooth or constricted, straight or attenuate, apex of trichome straight, curved or spiralled; apical cell tapered or often with a calyptra.[1]

1.	Trichomes not markedly attenuate at apex.	2
	Trichomes attenuate at apex.	*O. laetevirens*
2.	Trichomes twisted into a regular spiral.	*O. bonnemaisonii*
	Trichomes not spirally twisted.	3
3.	Trichomes 17–29μ dia.	*O. margaritifera*
	Trichomes 6–11μ dia.	*O. nigroviridis*

The species included here commonly occur on the mud flats associated with mangrove swamps and salt marshes.

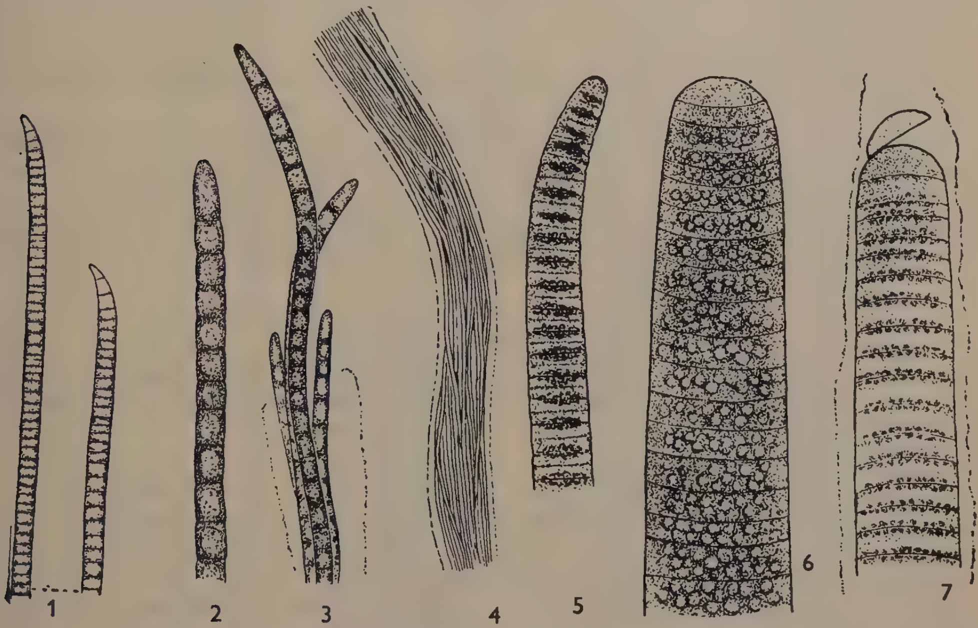

Fig. 3. 1, *Oscillatoria laetevirens* (× 613); 2–4, *Microcoleus chthonoplastes* (2, × 98; 3, 4, × 552); 5, *Oscillatoria nigroviridis* (× 552); 6, 7, *O. bonnemaisonii* (× 552). (All after Carter.)

(1) *Oscillatoria bonnemaisonii* Crouan

Crouan in Desmazières, *Pl. Crypt. Fr.*, Fasc. **2**, 537, 1858; Gomont, Mon. Oscill. p. 255, pl. 6, figs. 17, 18, 1893.

Trichomes pale olive-green, regularly or loosely twisted into a spiral, slightly torulose, apices not attenuate, end wall of terminal cell not thickened; cells 18–36μ dia., 3–6μ long. (Fig. 3, nos. 6, 7.)

Distribution: Local: salt marsh, Auckland, Eastbourne and probably on salt marshes elsewhere. General: more or less cosmopolitan.

(2) *Oscillatoria margaritifera* Kütz.

Kütz., *Tab. Phyc.* **1**, 51, pl. 43, fig. 10, 1845; Gomont, Mon. Oscill. p. 236, pl. 6, fig. 19, 1893.

Trichomes bright-olive green, flexible, torulose; apex of trichomes slightly attenuate, obtuse; apical cell capitate with a slightly convex calyptra; cells 17–29μ dia., 3–6μ long, transverse walls lined with granules. (Fig. 4, no. 3.)

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[1] The calyptra is formed by the outer thickened wall of the apical cell.

Distribution. Local: Hobson's Bay, Auckland. General: cosmopolitan.

(3) *Oscillatoria nigroviridis* Thwaites

Thwaites in Harvey, *Phyc. Brit.*, pl. 251 A, 1846–51; Gomont, Mon. Oscill. p. 237, pl. 6, fig. 20, 1893.

Plant mass dark olive-green; trichomes nearly straight, fragile, torulose, slightly curved at the extremities; apex of trichomes tapering, apical cell convex; transverse walls lined with granules; slightly thickened end wall; cells 6–11μ dia., 3–5μ long. (Fig. 3, no. 5.)

Distribution. Local: on rocks of upper littoral at Narrow Neck, Te Haruhi Bay, Stanmore, Rangitoto, Oneroa, Little Barrier, Gt Barrier. General: more or less cosmopolitan.

(4) *Oscillatoria laetevirens* Crouan

Crouan, Hist. des Algues Finist., **1**, 371, 1860; Gomont, Mon. Oscill., p. 246, pl. 7, fig. 11, 1893.

Plant mass thin, blue-green, trichomes yellowish green, straight, slightly torulose; apex briefly tapering, subobtuse, hooked, not capitate; cells 3–5μ dia., 2·5–5μ long; transverse walls granulated or contents uniformly granulated. (Fig. 3, no. 1.)

Distribution. Local: salt marsh and mangrove swamps, probably widely distributed. General: Europe, New England, Pacific North America, Polynesia.

Spirulina Turpin

Trichomes unicellular, without a sheath, forming a regular, more or less lax or close spiral; apex of trichome not tapering; cell contents homogeneous or slightly granular.

Spirulina subtilissima Kütz.

Kütz., *Phyc. Gen.* p. 183, 1843; Gomont, Mon. Oscill. p. 272, pl. 7, fig. 30, 1893.

Plant mass mucous, dark green, trichomes 0·6–0·9μ dia., agglutinated, flexuous, twisted into a very regular spiral 1·2–2·5μ dia., distance between turns 1·2–2μ, cell contents very pale green or yellowish. (Fig. 6, no. 3.)

Distribution. Local: Canoe Creek, Bay of Islands. General: Nebraska, California, Hawaii.

Phormidium Kütz.

Filaments forming a woolly or felt-like layer or rarely floating, parchment like or papery; trichomes many-celled, single within sheath; sheaths thin, partly or entirely diffluent; trichomes cylindrical, sometimes constricted at the joints; apex tapering, straight or uncinate, capitate or non-capitate, often with a calyptra.

1.	Apex of trichome straight, not capitate.	2
	Apex of trichome more or less curved, capitate.	*P. autumnale*
2.	Apical cell obtuse, conical, trichomes 3–5μ dia.	3
	Apical cell scarcely tapering, trichomes 4–6μ dia.	*P. ambiguum*
3.	Cells 2–4μ long.	*P. papyraceum*
	Cells 3·4–8μ long.	*P. corium*

(1) *Phormidium ambiguum* Gom.

Gomont, Mon. Oscill. p. 198, pl. 5, fig. 10, 1893.

Plant mass dark or yellowish green; filaments rigid, elongate, entangled; sheaths firm or mucous and diffluent, at times thick and lamellose; trichomes 4–6μ dia., slightly torulose; apices straight, not capitate; end wall slightly thickened; cells 1·5–2·7μ long, occasionally granular at cross walls. (Fig. 4, no. 4.) V.W.L. 101.

DISTRIBUTION. Local: on most muddy shores and marshes. General: more or less cosmopolitan.

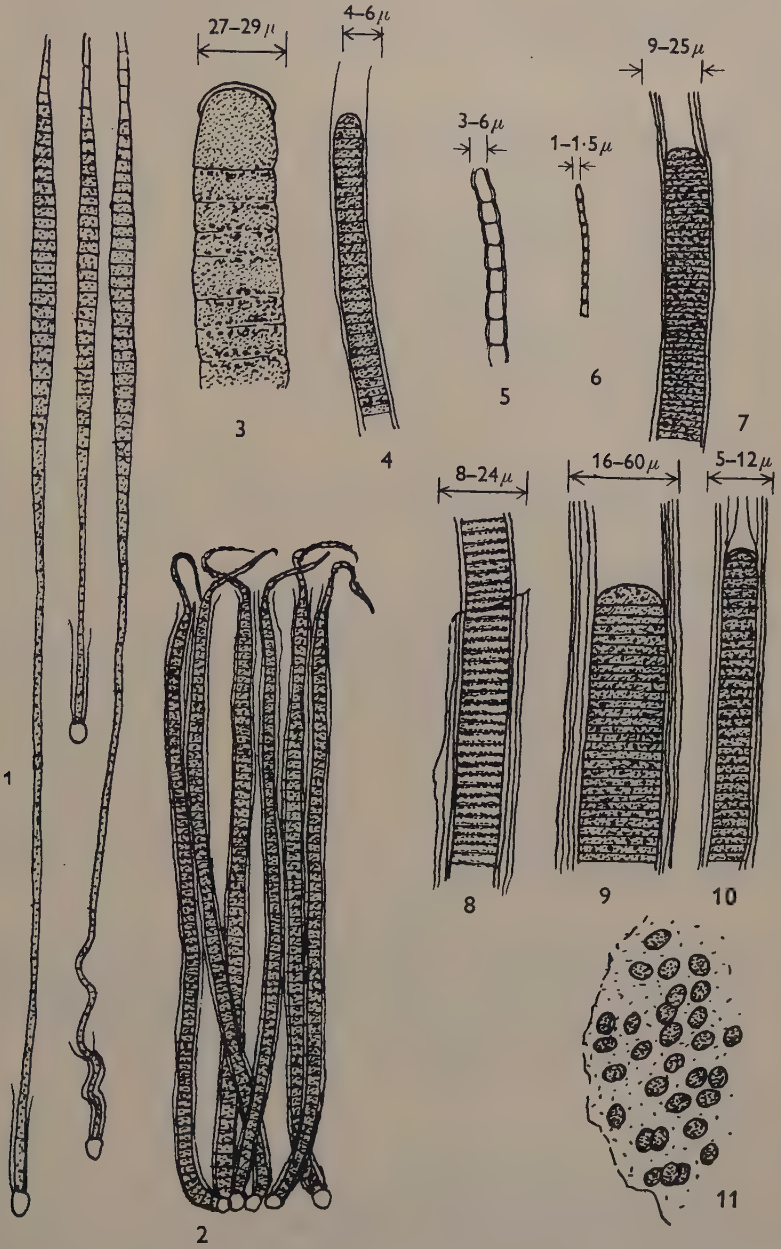

Fig. 4. 1, *Rivularia australis*; 2, *Isactis plana*; 3, *Oscillatoria margaritifera*; 4, *Phormidium ambiguum*; 5, *Schizothrix friesii*; 6, *S. lacustris*; 7, *Lyngbya confervoides*; 8, *L. aestuarii*; 9. *L. maiuscula*; 10, *L. semiplena*; 11, *Anacystis marina*. (×300.) (1, 2, after Womersley; 3–10, after Gomont; 11, original.)

(2) *Phormidium corium* (Ag.) Gom.

Gomont, Mon. Oscill. p. 192, pl. 5, figs. 1, 2, 1893.

Plant mass dark blue-green or black; filaments more or less flexuous, densely entangled; sheaths thin, separate or diffluent into an amorphous mass; trichomes 3·4–5μ dia., not torulose; apex straight, briefly tapering, not capitate; apical cell obtuse, conical; cells 3·4–8μ long; transverse walls conspicuous, not granulated. (Fig. 6, no. 1.)

Distribution. Local: upper littoral, Piha; Great Barrier Is., Porirua. General: cosmopolitan.

(3) *Phormidium papyraceum* (Ag.) Gom.

Gomont, Mon. Oscill. p. 193, 1893; Tilden, *Minn. Algae*, p. 101, pl. 4, figs. 73, 74, 1910.

Plant mass expanded, thin, leathery, fragile when dried, dark green; filaments elongate, strongly flexuous, very densely entangled; sheaths thin, papery, sometimes diffluent; trichomes 3–5μ dia., not constricted at joints; apex of trichome straight, briefly tapering, not capitate; apical cell obtuse-conical; calyptra absent; cells 2–4μ long, transverse walls usually conspicuous, not granulated. (Fig. 5, no. 1.) Supra-littoral.

Distribution. Local: spray zone (Piha) and probably elsewhere. General: Europe, New England, Hawaii, West Africa, Mauritius, St Paul Island.

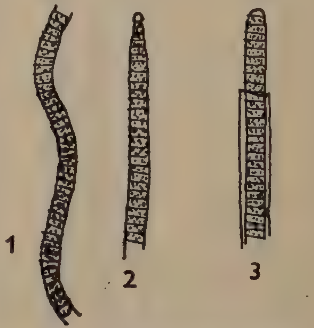

Fig. 5. 1, *Phormidium papyraceum*; 2, *P. autumnale*; 3, *Lyngbya lutea*. (All ×600.) (After Gomont.)

(4) *Phormidium autumnale* (Ag.) Gom.

Gomont, Mon. Oscill. p. 207, pl. 5, figs. 23, 24, 1893.

Plant mass expanded, fragile, dark blue-green, more rarely yellowish; filaments straight, rarely flexuous, entangled; sheaths narrow, fragile, mucous, distinct or diffluent into an amorphous, mucous, agglutinated mass; trichomes 4–7μ dia., not constricted at the joints; apex briefly tapering, straight or slightly curved, capitate; apical cell with a rotund calyptra; cells 2–5μ long; transverse walls frequently granulated. (Fig. 5, no. 2.) Supra-littoral.

Distribution. Local: spray zone (Piha) and probably elsewhere. General: Europe, U.S.A., Alaska, Faeroes, Iceland, Africa, Caucasus, Central Asia, West Indies, Borneo, Falkland Is., Graham Land.

Lyngbya C. Ag.

Filaments free and free-floating or forming an expanded floccose, caespitose mat, attached or free-floating; sheaths firm, of variable thickness, sometimes lamellose, colourless or rarely yellow-brown; trichomes sometimes torulose, obtuse or slightly tapering at apices; apical cell sometimes with a calyptra.

1.	Trichomes 2–6μ dia.	*L. lutea*
	Trichomes 5–60μ dia.	2
2.	Sheaths colourless.	3
	Sheaths coloured, yellow to dark yellow-brown.	*L. aestuarii*
3.	Trichomes 16–60μ dia., apex rounded, not capitate.	*L. maiuscula*
	Trichomes 10–25μ dia., apex not tapering, not capitate.	*L. confervoides*
	Trichomes 5–12μ dia., apex slightly tapering, capitate.	*L. semiplena*

(1) *Lyngbya aestuarii* Liebm.

Liebman, *Bemerk. Till. danske Algeflora*, 1841; Gomont, Mon. Oscill. p. 174, pl. 3, figs. 1, 2, 1893; Laing, *Trans. N.Z. Inst.* 57, 130, 1926; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 95, 1923.

Plant mass either forming a compact woolly layer on moist earth or a floccose floating mass, black or dull blue-green in colour; filaments long, flexible, twisted, densely crowded; sheaths thick, lamellate, colourless at first, later becoming yellowish or brownish; trichomes 8–24μ dia., not torulose; apices slightly attenuate, capitate, truncate; cells 2·7–5·6μ long, contents finely granular. (Fig. 4, no. 8.)

Distribution. Local: salt marshes and mangrove swamps. General: cosmopolitan.

(2) *Lyngbya maiuscula* (Dillw.) Harv.

Harvey in Hooker, *Brit. Flora,* **2** (1), 370, 1833; Gomont, Mon. Oscill. p. 151, pl. 3, figs. 3, 4, 1893.

Plant mass widely expanded, dark blue, blue-green, brownish or yellowish green; filaments long, often curled, moderately flexuous, sometimes cohering together; sheath broad, up to 11μ thick, colourless; trichomes 16–60μ dia., not constricted, cells 2–4μ long; apical cell round, calyptra absent. (Fig. 4, no. 9.)

Distribution. Local: upper littoral at Russell (edge of pools), Orewa, Stanmore, Whangaparaoa, Arran, Little Barrier, Gt Barrier, Fletcher's Bay. General: cosmopolitan.

(3) *Lyngbya confervoides* C. Ag.

C. Agardh, *Syst. Alg.* p. 73, 1824; Gomont, Mon. Oscill. p. 156, pl. 3, figs. 5, 6, 1893.

Plant mass caespitose, extended, fasciculate, dull yellowish or dark green, becoming violet on drying; filaments ascending from a decumbent and tangled base, long, straight; sheaths up to 5μ thick, colourless, later becoming lamellose; trichomes 9–25μ dia., not torulose; apex not attenuate; cells 2–4μ long; apical cell rotund, calyptra absent; transverse walls usually granulated. (Fig. 4, no. 7.)

Distribution. Local: in salt marshes, mangrove swamps and on mud-covered rocks; Orewa, Leigh, Cape Rodney, Oneroa, Little Barrier, Gt Barrier, Grassmere lagoon, Porirua, Eastbourne, Island Bay, Portobello. General: cosmopolitan.

(4) *Lyngbya semiplena* (C. Ag.) J. Ag.

J. G. Ag., *Alg. Mar. Med. Adr.* p. 2, 1842; Gomont, Mon. Oscill. p. 158, pl. 3, figs. 7–11, 1893.

Plant mass caespitose, extensive, usually dull yellowish green or dark green, becoming dark violet or yellowish on drying; filaments ascending from a decumbent and tangled base, soft, flexuous; sheaths to 3μ thick, colourless, becoming lamellose with age; trichomes 5–12μ dia., not torulose; apex slightly tapering, capitate; apical cell with calyptra; cells 2–3μ long; transverse walls usually granulated. (Fig. 4, no. 10.)

Distribution. Local: beach, Rangitoto and Russell Bay on buoy and launch bottom, Porirua, and probably elsewhere. General: cosmopolitan.

(5) *Lyngbya lutea* (Ag.) Gom.

Gomont, Mon. Oscill. p. 161, pl. 3, figs. 12, 13, 1893.

Plant mass more or less gelatinous, leathery, yellowish brown or olive, when dried often becoming dark violet; filaments coiled, flexuous, entangled; sheaths colourless, smooth at first, later up to 3μ thick and lamellose; trichomes 2·5–6μ dia., not constricted at joints; apex not tapering; apical cell with a rotund calyptra; cells 1·5–5·5μ long; transverse walls indistinct; cell contents granular. (Fig. 5, no. 3.)

Distribution. Local: on upper littoral rocks on beach, Russell, and probably elsewhere. General: Europe, U.S.A., West Indies, Faeroes, Mediterranean, Chile, North Africa, South Australia and probably elsewhere.

Symploca Kütz.

Filaments branched, ascending from a prostrate base, agglutinated together in fascicles, more or less procumbent and coalescing; false branches solitary; sheaths thin, colourless, firm or somewhat mucous; apex of trichome straight, sometimes a little tapering; outer membrane of apical cell slightly thickened in some species.

Symploca laeteviridis Gom.

Gomont, Mon. Oscill. p. 129, pl. 2, figs. 6–8, 1893.

Plant mass thin, fibrillose, light green or yellowish; fascicles up to 1 mm. high, slender; filaments moderately flexuous, somewhat parallel, agglutinated, not branched; sheaths wide, somewhat mucous; trichomes 1·5–3·5μ dia., torulose, apical cell conical; cells 2·5–6μ long. (Fig. 6, no. 2.)

Distribution. Local: rocks of middle to upper littoral, Stanmore Bay, Howick, Narrow Neck. General: Alaska, Florida.

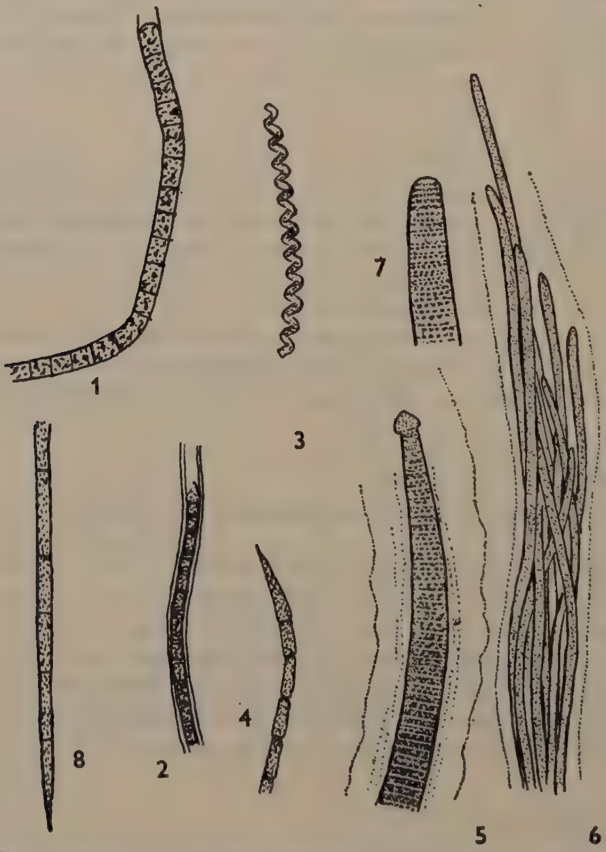

Fig. 6. 1, *Phormidium corium*; 2, *Symploca laeteviridis*; 3, *Spirulina subtilissima*; 4, *Microcoleus tenerrimus*; 5–7, *Hydrocoleus lyngbyaceus*; 8, *Microcoleus acutissimus*. (8, ×218; 4, 9, 10, ×545; 1–3, 5, ×500–700; 8, ×1000.) (1, 2, 4, after Gomont; 3, 5–7, after Carter; 8, after Drouet.)

Hydrocoleus Kütz.

Plant mass caespitose, rarely hardened with lime, or forming a flat membrane; sheaths colourless, somewhat lamellose, more or less mucous, later diffluent; trichomes few within sheath, often loosely aggregated; apex of trichome straight, tapering, capitate, with a calyptra.

Hydrocoleus lyngbyaceus Kütz.

Kütz., *Sp. Alg.* p. 259, 1849; Gomont, Mon. Oscill. p. 75, pl. 12, figs. 8–10, 1893.

Plant mass caespitose or mucous, dark green, usually epiphytic; filaments adnate, unbranched at base, branched higher up; false branches numerous; sheaths wide, mucous, roughened in outline, tapering to apex, sometimes diffluent; trichomes 8–16μ dia., not torulose, numerous at base of filament, solitary towards apex, sometimes spirally twisted; apex tapering, truncate; cells 2·5–4·5μ long; transverse walls granulated. V.W.L. 276.

Distribution. Local: *Lichina* zone, Stanmore Bay; on *Melobesia*, Pihama. General: cosmopolitan.

Distributed in Fasc. 12 Herb. Lind. Exsicc. as *Symploca hydnoides*.

Schizothrix Kütz.

Plants living on moist earth or on rocks, rarely entirely aquatic, filaments forming erect fascicles or a prostrate pannose stratum, rarely free-floating; sheaths first colourless, later yellow brown, purplish pink or bluish.

1.	Trichomes 3–6μ.	*S. friesii*
	Trichomes 1–1·5μ.	*S. lacustris*

(1) *Schizothrix friesii* Gom.

Gomont, Mon. Oscill. p. 54, pl. 9, figs. 1, 2, 1893.

Plant mass indefinite, expanded, black, olive or lead-coloured, filaments in lower portions twisted and entangled, in upper parts somewhat straight, parallel, dichotomously divided, forming rigid, erect, spine-like tufts up to 3 cm. high; sheaths firm, pointed at apex, lamellose; trichomes 3–6μ dia., torulose, 1 or more within each sheath; apical cell conical, cells 4–11μ long with granular contents. (Fig. 4, no. 5.)

Distribution. Local: mangrove swamp, Birkdale and probably in similar localities elsewhere. General: cosmopolitan.

(2) *Schizothrix lacustris* A. Br.

Gomont, Mon. Oscill. p. 39, pl. 6, figs. 9–12, 1893.

Plant mass cushion-shaped, dull yellowish green; filaments flexuous, closely crowded, mass broadening towards apex and becoming branched into many parts; branches twisted, entangled or somewhat parallel; sheaths wide, colourless; trichomes 1–1·5μ dia., torulose, numerous in basal part of filament, few above, often spirally twisted; cells up to 4μ long. (Fig. 4, no. 6.)

Distribution. Local: Piha with *Dichothrix gypsophila* (p. 369). General: U.S.A.

Microcoleus Desm.

Filaments simple or branched, creeping on the ground or growing among other algae; sheaths colourless, not lamellose, sometimes diffluent; trichomes numerous in sheath, closely crowded, often intertwisted; apex of trichome straight, tapering; apical cell commonly acute.

1.	Trichomes 1·7–2·3μ dia., not constricted at joints.	*M. acutissimus*
	Trichomes 1·5–2μ dia., constricted at joints.	*M. tenerrimus*
	Trichomes 2·5–6μ dia.	*M. chthonoplastes*

(1) *Microcoleus acutissimus* Gardn.

Gardner, *Mem. N.Y. Bot. Gard.* 7, 55, pl. 11, fig. 2, 1927.

Filaments forming a mat or mixed with other algae, simple or branched, often more or less flexuose; filaments broad, mucous with acute apices; trichomes elongate, fragile, loosely aggregated, scarcely constricted at the joints, 1·7–2·3μ dia., cells 3·5–8μ long; walls scarcely distinct, frequently granulate; apical cell long, acutely conical. (Fig. 6, no. 8.)

Distribution. Local: mangrove swamp, Russell, Stanmore Bay (upper littoral), Narrow Neck and probably elsewhere. General: Brazil, North America, West Indies (Jamaica) and probably elsewhere.

(2) *Microcoleus tenerrimus* Gom.

Gomont, Mon. Oscill. p. 93, pl. 14, figs. 9–11, 1893.

Filaments simple or slightly branched, densely entangled or mixed with other algae; sheaths wide, irregular in outline, pointed or open at apex, sometimes entirely diffluent, trichomes 1·5–2μ dia., constricted at joints, long, flexuous, more or less numerous within the sheath; apex of trichome often tapering gradually; apical cell very acute, conical, not capitate; cells 2·2–6μ long. (Fig. 6, no. 4.)

Distribution. Local: Stanmore Bay (upper littoral), and probably elsewhere. General: more or less cosmopolitan.

(3) *Microcoleus chthonoplastes* Thur.

Thuret, *Ann. Sci. Nat. Bot.* (6), **1**, 378, 1875; Gomont, Mon. Oscill. p. 91, pl. 4, figs. 5–8, 1893.

Plant mass a dark, olive-green, expanded layer on damp mud or mixed with other algae; filaments twisted, rarely branched; sheaths cylindrical, tapering at both extremities, usually open, trichomes blue-green, short, nearly straight, numerous within the sheath, torulose, apex attenuate; apical cell acute, conical; cells 2·5–6μ wide, 3·6–10μ long. (Fig. 3, nos. 2–4.)

Distribution. Local: probably common on most mangrove swamps: recorded from Russell, Auckland and Porirua. General: cosmopolitan.

NOSTOCACEAE

Sheaths forming a confluent, gelatinous or membranaceous integument or else absent; trichomes of a single row of uniform cells, with heterocysts, usually twisted or entangled, not branched, with no differentiation into base and apex; reproduction by hormogones and gonidia.

1.	Filaments united into colonies of a definite form with a firm epidermal layer.	*Nostoc*
	Filaments free or adherent but not in a colony of definite form.	2
2.	Cells disk-shaped, shorter than diameter.	*Nodularia*
	Cells spherical or oval, longer than diameter.	*Anabaena*

Nostoc Vaucher

Plant mass at first globose, later becoming irregular, solid or hollow, mucous, gelatinous or leathery; filaments flexuous, curved, entangled; sheaths distinct or invisible; trichomes commonly torulose; cells depressed-spherical, barrel-shaped or cylindrical; heterocysts intercalary; gonidia spherical or oblong, located in series between heterocysts.

1.	Microscopic, among and in the cells of other algae.	*N. entophytum*
	Macroscopic, forming gelatinous masses among other algae or on soil.	2
2.	Mature colonies an irregular membranous sheet, trichomes 4–5·6μ dia.	*N. commune*
	Mature colonies spherical or solid, tuberculate.	3
3.	Mature colonies irregular, trichomes 4–5μ dia.	*N. sphaericum*
	Mature colonies spherical.	4
4.	Trichomes 3·5–4μ dia.	*N. linckia*
	Trichomes 5–8μ dia.	*N. microscopicum*

(1) *Nostoc entophytum* Born. & Flah.

Born. & Flah., *Ann. Sci. Nat. Bot.* (7), 7, 190, 1888; Laing, *Trans. N.Z. Inst.* 7, 130, 1926; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 96, 1923.

Thallus minute, among and in the cells of other algae; sheath distinct, hyaline or dingy brown; trichomes 2·5–3μ broad, torulose; vegetative cells flattened or spherical; heterocysts larger; spores spherical or flattened, 5–6μ wide, 8μ long.

DISTRIBUTION. Local: in *Lyngbya aestuarii* at the Bluff. General: cosmopolitan.

(2) *Nostoc commune* Vaucher

Vaucher, *Hist. des Conferves d'eau douce*, p. 222, pl. 16, fig. 1, 1803; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), 7, 203, 1888.

Plant mass gelatinous, at first spherical, later becoming flattened into an undulating, membranous, entire or torn, often perforated sheet; blue-green, olive, or brown in colour; filaments flexuous, entangled; sheaths brownish near surface, more or less distinct throughout; trichomes 4·5–6μ dia.; cells depressed-spherical or barrel-shaped; heterocysts 7μ dia., often up to 3–5 in number. (Fig. 7, no. 2.)

DISTRIBUTION. Local: Russell, Stanmore, Rangitoto and probably elsewhere. General: cosmopolitan.

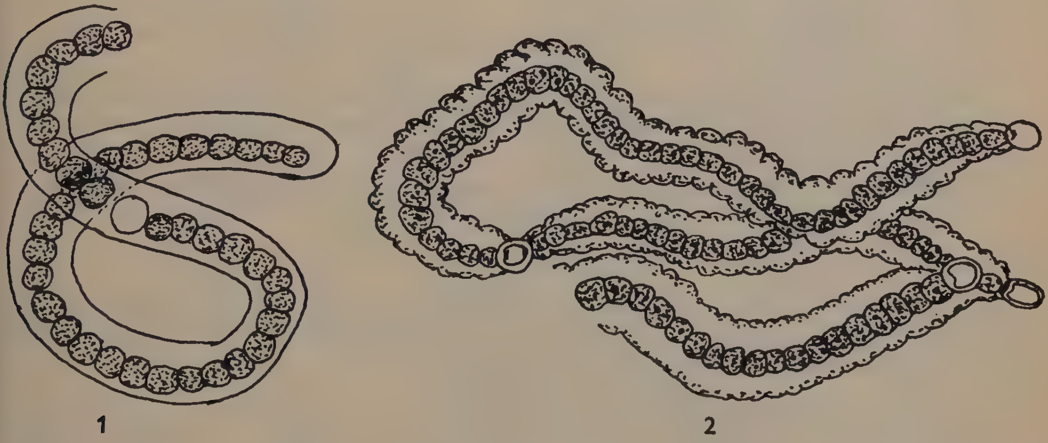

Fig. 7. 1, *Nostoc microscopicum*; 2, *Nostoc commune*. (×600.) (1, after Cooke; 2, after Hansgirg.)

(3) *Nostoc sphaericum* Vaucher

Vaucher, *Hist. des Conferves d'eau douce*, p. 223, pl. 16, fig. 2, 1803; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), 7, 208, 1888.

Colonies, spherical, 1–15 mm. rarely 6–7 cm. dia., later becoming irregularly tuberculate, solid, surrounded by a firm outer layer, olive-green, yellowish violet or brownish; filaments flexuous, densely interwoven; trichomes 4–5μ dia.; heterocysts 6μ dia.; spores 5μ wide, 7μ long, wall thick, smooth and brownish. (Fig. 8, no. 5.)

DISTRIBUTION. Local: Frenchman's Creek, Onewhero, Hobson's Bay (Auckland) and probably elsewhere. General: Iceland, Scandinavia, Europe, Mediterranean, North America, West Indies, Montevideo, Australia.

(4) *Nostoc microscopicum* Carm. ex Harv.

Harvey in Hooker, *Brit. Flora*, 2, 399, 1833; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), 7, 210, 1888.

Colonies spherical or oblong, rarely beyond 1 cm. dia., soft, olive or brownish; filaments loosely entangled; sheaths more or less distinct, yellowish; trichomes 5–8μ dia., cells somewhat spherical; heterocysts more or less spherical, 7μ dia.; gonidia 6–7μ dia., 9–15μ long, wall smooth; cell contents sky blue or violet-green. (Fig. 7, no. 1.)

Distribution. Local: cave, Piha. General: more or less cosmopolitan.

(5) *Nostoc linckia* Born.

Newton, *Handb. Brit. Seaw.* p. 44, fig. 30, 1931; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **7**, 192, 1888.

Colonies roundish, becoming brownish with age; filaments contorted or intertwined, enclosed in a conspicuous sheath; trichomes 3·5–4μ dia.; cells spherical or flattened; heterocysts 5–6μ dia.; spores in series on either side of heterocysts, 7–8$\mu \times$ 6–7μ, wall smooth, hyaline or brownish. (Fig. 8, no. 6.)

Distribution. Local: Hobson's Bay, probably elsewhere. General: more or less cosmopolitan.

Nodularia Mertens

Filaments free; sheaths colourless, usually thin, mucous, sometimes diffluent; trichomes more or less straight, moniliform; cells short, depressed, disk-shaped; heterocysts depressed; gonidia spherical to disk-shaped, developed in series between heterocysts, walls smooth.

Nodularia harveyana (Thwaites) Thur.

Thuret, *Ann. Sci. Nat. Bot.* (6), **1**, 378, 1875; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **7**, 243, 1888.

Filaments 4–6μ dia., much curved, terminated by an obtuse conical cell; sheaths thin, colourless, distinct; cells about as long as broad; heterocysts subquadrate; gonidia 8μ dia., yellowish brown. (Fig. 8, no. 4.)

Distribution. Local: upper littoral at Stanmore Bay, Orewa, Fletcher's Bay, Whangaparapara. General: more or less cosmopolitan.

Anabaena Bory

Sheaths absent or when present diffluent; trichomes usually rigid and fragile, free or aggregated to form a flocculent mass; cells quadratic or longer than broad; heterocysts numerous, intercalary; gonidia variously disposed.

1. Gonidia oval or spherical, not contiguous to heterocysts. *A. variabilis*
   Gonidia cylindrical, contiguous to heterocysts. *A. torulosa*

(1) *Anabaena variabilis* Kütz.

Kütz., *Phyc. Gen.* p. 210, 1843; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **7**, 226, 1888.

Plant mass gelatinous, on damp soil or free-floating, dark green; trichomes 4–6μ dia., flexuous, slightly torulose; cells 2·5–6μ dia., quadrate, terminal cell obtuse, conical; heterocysts 6μ wide, 8μ long; gonidia 7–9μ wide, 8–14μ long, numerous, in series remote from heterocysts; wall of mature gonidium smooth, yellowish brown. (Fig. 9, no. 3.)

Distribution. Local: Rangitoto, Hobson's Bay. General: cosmopolitan.

(2) *Anabaena torulosa* (Carm.) Lagerh.

Lagerheim, *Öfvers VetenskAkad. Förh., Stockh.*, **2**, 37, 1883; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **7**, 236, 1888; Laing, *Trans. N.Z. Inst.* **57**, 130, 1926; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 96, 1923.

Plant mass thin, blue-green; trichomes free, simple, moniliform, 4·2–5μ dia., cells as long as or shorter than broad; heterocysts 6μ wide, 6–10μ long, spherical or ovoid; spores 7–12μ wide, 18–28μ long, cylindrical, adjacent to heterocysts and developing centrifugally, wall smooth, greyish. (Fig. 8, no. 1.)

Distribution. Local: common generally; Bluff, with *Lyngbya aestuarii*. General: cosmopolitan.

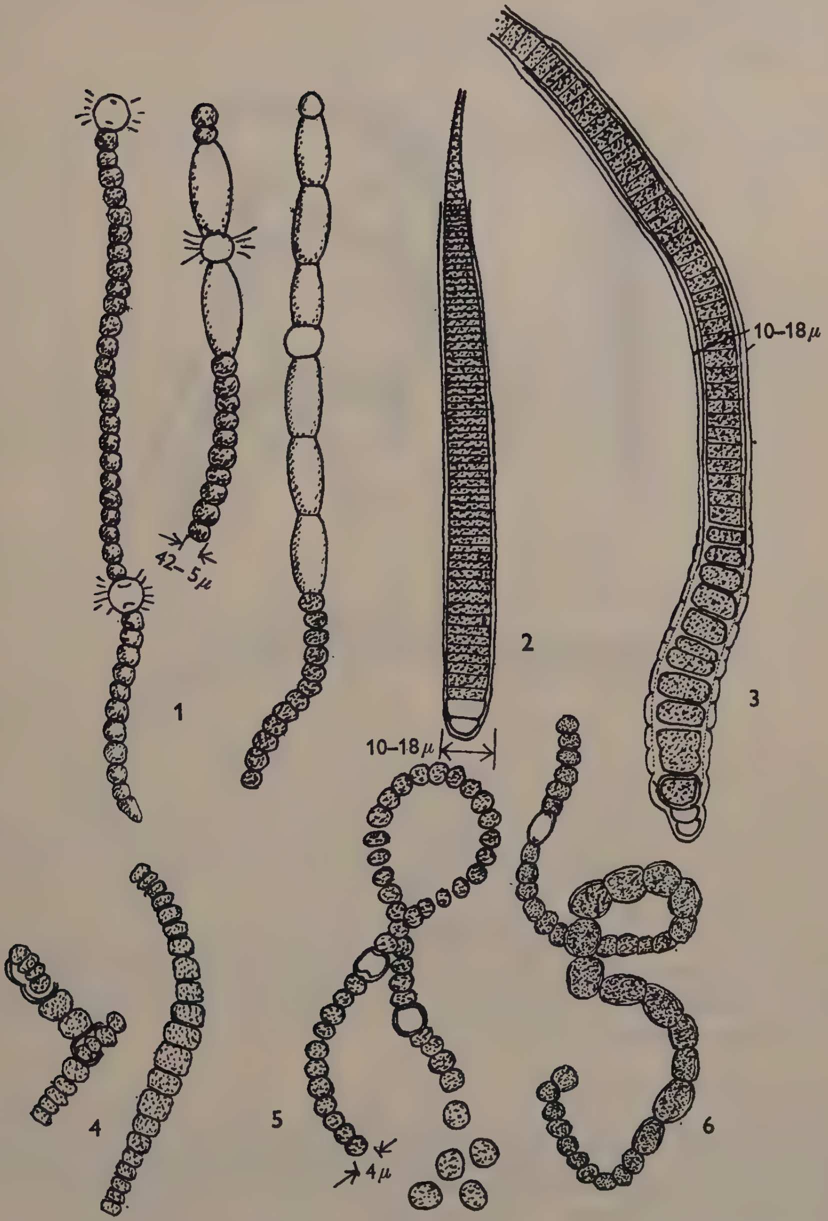

Fig. 8. 1, *Anabaena torulosa*; 2, *Calothrix confervicola*; 3, *Calothrix scopulorum*; 4, *Nodularia harveyana*; 5, *Nostoc sphaericum*; 6, *Nostoc linckia*. (All × 500–700.) (1, 5, after Cooke; 2, 3, 4, and 6, after Bornet & Thuret.)

SCYTONEMATACEAE

Filaments with false branches formed by perforation of sheath, each branch developing its own sheath; sheaths homogeneous and colourless or lamellose and yellowish or brownish; trichomes one or more within each sheath; heterocysts and gonidia variously disposed; reproduction by hormogones and gonidia.

1.	Heterocysts absent.	*Plectonema*
	Heterocysts present.	**2**
2.	False branching arising between two heterocysts.	*Scytonema*
	False branching arising in immediate vicinity of heterocysts.	*Tolypothrix*

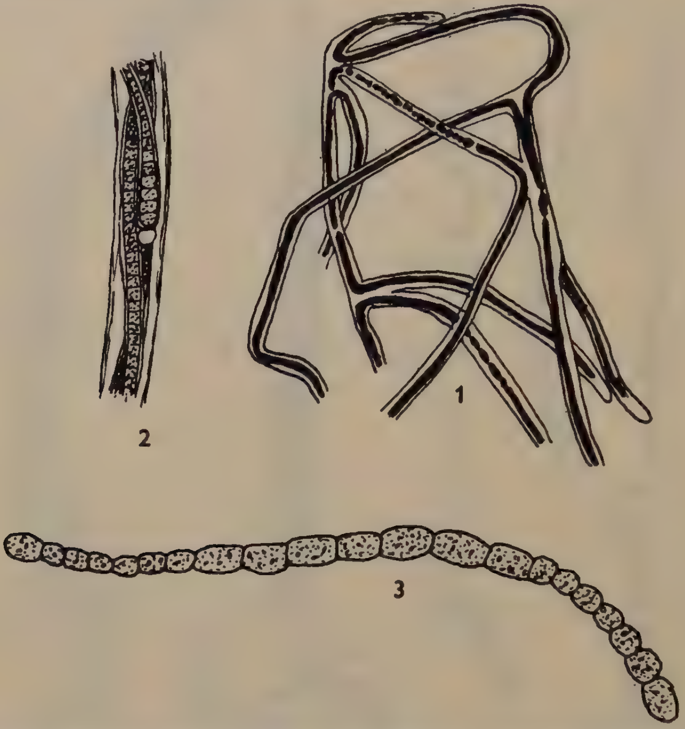

Fig. 9. 1, *Scytonema tolypotrichoides*; 2, *Dichothrix orsiniana*; 3, *Anabaena variabilis*. (1, after Wood; 2, after West; 3, after Hansgirg.) (1, × 500; 2, × 210; 3, × 500.)

Plectonema Thur.

Filaments free or forming felt-like masses, branched; false branches solitary or in pairs; sheaths firm, colourless or rarely yellowish orange; trichomes often constricted at joints; apex of trichome straight, rarely tapering.

Plectonema nostocorum Bornet.

Gomont, Mon. Oscill. p. 122, pl. 1, fig. 11, 1893.

Filaments elongate, more or less straight, much or sparingly branched; false branches solitary or in pairs; sheaths thin, colourless; trichomes 1–1·5μ dia., constricted at joints; apical cell rotund; cells 2–2·5μ long. (Fig. 10.)

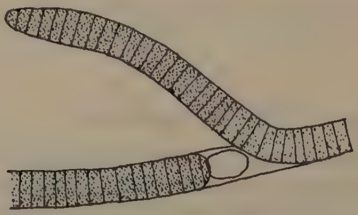

Fig. 10. *Plectonema nostocorum*. (After Gom.) (× 700.)

Distribution. Local: in sheaths of other Myxophyceae (*Rivularia*, *Dichothrix*), Piha. General: more or less cosmopolitan. Primarily a fresh-water species.

Scytonema Ag.

Filaments branched; false branches usually arising between two heterocysts, solitary or in pairs; trichomes single within sheath, straight; hormogones terminal, solitary; gonidia rare, spherical or oval with smooth wall.

Scytonema tolypotrichoides Kütz.

Kütz., *Sp. Alg.* p. 307, 1849; Born. & Flah., *Ann. Sci. Nat. Bot.*, (7), **5**, 100, 1887.

Plant mass caespitose, floating, spherical, brown or green; filaments 10–15μ dia., 5–6 mm. long, radiating from centre, repeatedly branched; sheaths colourless, becoming orange-brown, lamellose; trichomes 8–12μ dia., cells somewhat quadrate, hardly visible; heterocysts varied in length; cell contents densely granular. (Fig. 9, no. 1.)

Distribution. Local: Canoe Creek. General: U.S.A., Europe.

Tolypothrix Kütz.

Filaments branched; false branches usually arising in immediate region of the heterocysts; sheaths somewhat thin, flexible; gonidia spherical, oval or elliptical, often many in a series; wall of gonidium smooth, thin.

Tolypothrix irregularis Berk.

Berk. in Hooker, *Fl. Nov. Zel.*, **2**, 265, 1855; Laing, *Trans. N.Z. Inst.* **57**, 131, 1926; J. Ag., De Alg. Nov. Zel. Mar. p. 1, 1877.

Filaments blue-green, irregular, compressed, sometimes constricted or torulose, often attenuated above and below, furnished at the base with a minute, hyaline, elliptic connecting point.

Distribution. Local: Stewart Is. and possibly elsewhere. General: endemic.

An endemic species recorded by Colenso as occurring on tidal mud flats amongst patches of *Vaucheria*. This is the only endemic Myxophycean from marine waters in New Zealand. In view of the generally cosmopolitan character of most species, this record is regarded as doubtful and search should be made for the plant.

Rivulariaceae

Filaments tapering from base to apex, terminating in a colourless hair; branching false, branches due to development of new trichome, usually immediately under an intercalary heterocyst, either forming a new sheath and separating or remaining for a time within the original sheath; heterocysts usually basal, sometimes intercalary; reproduction by hormogones and gonidia.

1.	Filaments free or coalesced into a branched plant mass.	2
	Filaments coalesced into a gelatinous spherical or hemispherical plant mass.	3
2.	Filaments simple or branched; false branches distinct.	*Calothrix*
	Filaments branched; false branches several, remaining within original sheath.	*Dichothrix*
3.	Heterocysts basal.	4
	Heterocysts intercalary.	*Brachytrichia*
4.	Trichomes radiating from the base within a globular or lobed thallus.	*Rivularia*
	Trichomes parallel in a flattened thallus.	*Isactis*

Calothrix Agardh

Plant mass of penicillate tufts or a soft velvety expansion; filaments simple or slightly branched; heterocysts basal or intercalary; gonidia basal, in rows.

1.	Heterocysts basal.	2
	Heterocysts basal and intercalary.	5
2.	Plants fasciculate or penicillate, parasitic.	*C. confervicola*
	Plants caespitose, often on rocks.	3
3.	Filaments 10–18μ.	4
	Filaments 15–20μ.	*C. pulvinata*
4.	Trichomes 8–15μ.	*C. scopulorum*
	Trichomes 5–10μ.	*C. parietina*
5.	False branches in pairs arising between two heterocysts.	*C. vivipara*
	Filaments unbranched, or branches solitary.	6
6.	Filaments 10–40μ dia., trichomes not ending in a hair.	*C. pilosa*
	Filaments 12–40μ dia., trichomes terminating in a hair.	7
7.	Filaments 15–18μ dia., sheaths ocreate.	*C. prolifera*
	Filaments 12–40μ dia., ocreae absent.	*C. crustacea*

(1) *Calothrix confervicola* (Roth) C. Ag.

C. Ag., *Syst. Alg.* p. 70, 1824; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **3**, 349, 1886; Laing, *Trans. N.Z. Inst.* **57**, 131, 1926; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 97, 1923.

Filaments gregarious, fasciculate, not thickened at base, attached to other algae, 12–25μ dia., 2–3 mm. long; sheaths close, colourless or yellowish brown below, soft, gelatinous, free or united at base, unbranched; trichomes 10–18μ dia., cells 4–5 times shorter than broad; heterocysts 1–2, basal; hormogones numerous. (Fig. 8, no. 2.)

Distribution. Local: Three Kings Is., Wellington (on *Chaetomorpha aerea*), Bluff (on *Ectocarpus*), Chatham Is. General: cosmopolitan. (De Capra recorded it on *Stilophora* at the Bluff, but this record is doubtful.)

(2) *Calothrix scopulorum* (Weber & Mohr) C. Ag.

C. Ag., *Syst. Alg.* p. 70, 1824; J. Ag., De Alg. Nov. Zel. Mar. p. 1, 1877; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **3**, 353, 1886; Hooker, *Fl. Nov. Zel.* **2**, 265, 1856; *Handb. N.Z. Flora*, p. 720, 1867; Laing, *Trans. N.Z. Inst.* **57**, 131, 1926.

Plant mass caespitose, velvety, olive-green; filaments contorted, erect, up to 1 mm. long, thickened at base, 10–18μ dia.; sheaths thick, colourless, yellow-brown or zoned, lamellose; trichomes 8–15μ dia., ending in a hair; heterocysts 1–3, basal; hormogones numerous, 4–5 times longer than broad. (Fig. 8, no. 3.)

Distribution. Local: Stanmore Bay, Narrow Neck, on muddy rocks near high water mark, Howick, Orewa, Whangaparaoa, Little Barrier. General: cosmopolitan.

(3) *Calothrix vivipara* Harv.

Harvey, Ner. Bor. Amer. 106, 1857; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **3**, 362, 1886.

Plant mass widely expanded, velvety, blackish green; filaments 12–24μ dia., 3–5μ long, interwoven and decumbent at base, erect portion flexuous, branched; false branches numerous, often in pairs; sheaths thick, gelatinous, yellowish brown; trichomes 9–15μ dia., tapering gradually from base to apex and terminating in a hair; heterocysts basal and intercalary, 2–4 seriate; cell contents olive-green.

Distribution. Local: salt marsh, Hobson's Bay (Auckland). General: New England. This species is probably more widely distributed throughout the world than present records indicate.

(4) *Calothrix crustacea* Thur.

Thuret, *Notes Algol.* **1**, 13, pl. 4, 1878; Born. & Flah. *Ann. Sci. Nat. Bot.* (7), **3**, 359, 1886.

Plant mass caespitose, expanded, velvety, blackish green or brownish; filaments 12–40μ dia., 1–2 mm. long, erect; sheaths somewhat thick, colourless or yellowish brown, lamellate when old, expanded and dilated in upper part; trichomes 8–15μ dia., terminating in long hair; heterocysts 1–3 at base and intercalary; hormogones numerous; gonidia oblong, in series. (Fig. 12, no. 1.)

Distribution. Local: Bay of Islands, Hokianga mangroves, Orewa, Howick, Arkles Bay, Bluff, on *Chaetomorpha*; Stewart Is. General: more or less cosmopolitan.

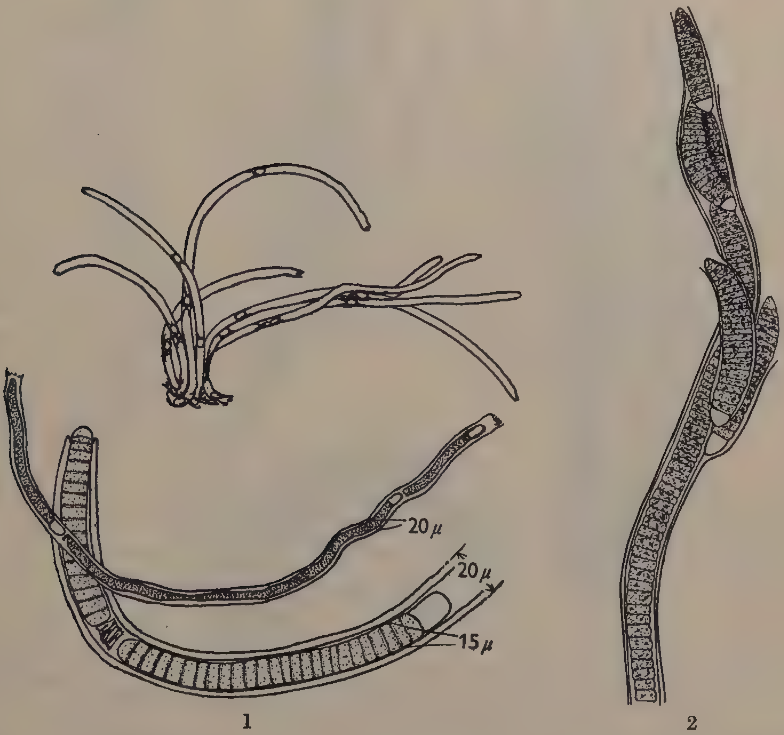

Fig. 11. (1) *Calothrix pilosa.* (2) *Calothrix pulvinata.* (× 700.) (After Bornet & Thuret.)

(5) *Calothrix pulvinata* (Mert.) Ag.

Tilden, *Minn. Algae*, p. 260, pl. 16, fig. 14, 1910; Nordst., *K. svenska VetenskAkad. Handl.* **22** (8), 72, 1888.

Plant mass sponge-like, porous, fasciculate, hairy on the surface, dull green, widely expanded; filaments 15–20μ dia., erect, flexuous, scarcely thickened at the base, agglutinated into irregular fascicles, sparingly branched; branches often opposite; sheaths thick, firm, lamellose, colourless or brownish; trichomes 8–12μ dia., tapering to a short hair; cells 2–3 times shorter than wide. (Fig. 11, no. 2.)

Distribution. Local: Hokianga on mangroves, Lyttelton. R.M.L. 1776 (no locality). General: Europe, U.S.A., Chile, Adriatic.

(6) *Calothrix pilosa* Harv.

Harvey, Ner. Bor. Amer. 106, pl. 48C, 1858.

Plant mass caespitose, widely expanded, black or dark blue-green; filaments 10–40μ dia., 2–10 mm. long, decumbent and interwoven at base, erect at the apices, elongate, rigid, free or in fascicles, distinctly thicker in the upper parts; sheaths thick, at first orange, finally yellowish brown, opaque; trichomes 10–20μ dia., briefly tapering at the apex, terminating in a hemispherical cell. (Fig. 11, no. 1.)

DISTRIBUTION. Local: Bluff (90 Mile Beach) Stanmore, Stewart Is. (on *Chaetomorpha*). General: U.S.A., West Indies, Red Sea, Guadeloupe, Mauritius.

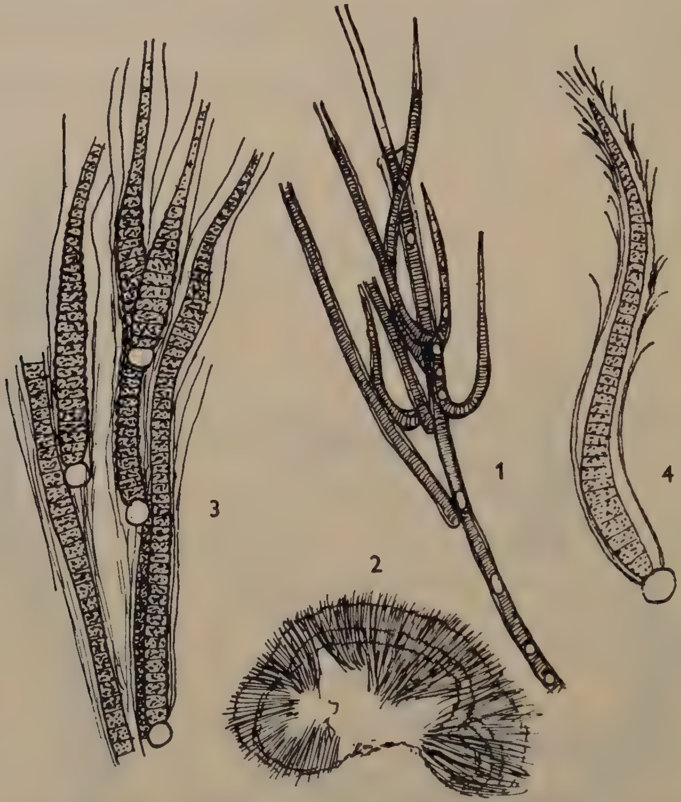

Fig. 12. 1, *Calothrix crustacea*; 2, section of thallus, *Rivularia polyotis*; 3, trichomes of *R. polyotis*; 4, *Calothrix parietina*. (1, 3, 4, × 500.) (After Bornet & Thuret.)

(7) *Calothrix parietina* (Naeg.) Thur.

Thuret, *Ann. Sci. Nat. Bot.* (6), **1**, 381, 1875.

Filaments 10–12μ dia., scattered or aggregated into a crustaceous, thin, brown or black mass, erect or decumbent, flexuose, contorted, commonly uniform in dia.; sheaths somewhat thick, yellowish brown, opaque, uniform or ocreate; ocreae when present wide and fringed in upper parts; trichomes 5–10μ dia., ending in a thin hair; cells 2–3 times wider than long; intercalary heterocysts rare. (Fig. 12, no. 4.)

DISTRIBUTION. Local: spray zone (Piha), Whangaparapara. General: Europe, U.S.A., North Africa, India, Mediterranean, Greenland, Australia.

(8) *Calothrix prolifera* Flah.

Born. & Flah. *Ann. Sci. Nat. Bot.* (6), **3**, 361, 1886; Tilden, *Minn. Alg.* p. 262, 1910; Frémy, Cyanophycées des Côtes d'Europe, p. 147, pl. 38, fig. 3, 1934.

Plant mass expanded, velvety, brownish green; filaments 15–18μ dia., 2 mm. long, somewhat flexuous, curved and thickened at the base, branched here and there, branches arising in vicinity of heterocyst; sheaths thick, lamellose, firm, colourless above, yellowish below, ocreate, ocreae dilated and torn; trichomes 8–12μ dia., tapering to a hair; cells 3–4 times shorter than long; heterocysts scattered.

Distribution. Local: Orongo Bay. General: California, Mediterranean.

This appears to be a rare species and the only other recorded localities are Banyuls, Gibraltar and Alameda in California.

Dichothrix Zanard.

Plant mass caespitose, penicillate or pulvinate; filaments more or less dichotomously branched; trichomes often 2–6, enclosed within original sheath; heterocysts basal or intercalary.

1.	Sheaths close, gradually tapering at apex.	*D. orsiniana*
	Sheaths lamellose, funnel-shaped at apex.	*D. gypsophila*

(1) *Dichothrix orsiniana* (Kütz.) Born. & Flah.

Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **3**, 376, 1886.

Plant mass caespitose, composed of penicillate fascicles, 2–3 mm. long, gelatinous, dark green; filaments 10–12μ dia., flexuous, erect, radiating; false branches appressed, enclosed for some distance in common tegument; sheaths thick, close, soft, yellow, in lower parts brownish and opaque; trichomes 6–7·5μ dia., ending in a hair, cell contents olive-green; heterocysts basal. (Fig. 9, no. 2.)

Distribution. Local: Frenchman's Creek. General: New England, Florida.

The plants were young but were identified by Dr Drouet as being probably of this species.

(2) *Dichothrix gypsophila* (Kütz.) Born. & Flah.

Born. & Flah. *Ann. Sci. Nat. Bot.* (7), **3**, 377, 1886.

Filaments caespitose, encrusted with lime, 15–18μ dia., about 2 mm. long, erect, penicillate; upper false branches appressed and contained within parent sheath; sheaths thick, lamellose, smooth, orange, later becoming brown and opaque, trichomes 6–14μ dia., gradually tapering into a hair; cells as long as or longer than broad; heterocysts usually 2–3 in a series. (Fig. 13, no. 1.)

Distribution. Local: Piha, rocks with fresh water dripping from above. General: U.S.A.

Rivularia (Roth) Ag.

Colonies spherical, hemispherical or variously lobed, solid or hollow, sometimes confluent; filaments radiating from the centre, repeatedly branched; sheaths distinct near base of trichomes, near edge of colony becoming gelatinous and confluent; heterocysts basal; gonidia, when present, more or less cylindrical.

1.	Thallus solid, compact.	3
	Thallus hollow, soft.	2
2.	Trichomes 1–3μ below, 5–7·5μ above.	*R. australis*
	Trichomes 2–5μ below, 8–13·5μ above.	*R. polyotis*
3.	Trichomes 2·5–6μ.	*R. atra*
	Trichomes 7–9μ.	*R. vieillardii*

(1) *Rivularia atra* Roth

Roth, *Cat. Bot.* **3**, 340, 1806; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **4**, 353, 1886; Nordst., *K. svenska VetenskAkad Handl.* **22** (8), 73, 1888.

Thallus solitary or confluent, hemispherical or flattened, solid; trichomes radiating from centre, abundantly falsely branched; trichomes 2·5–5μ below, expanding to

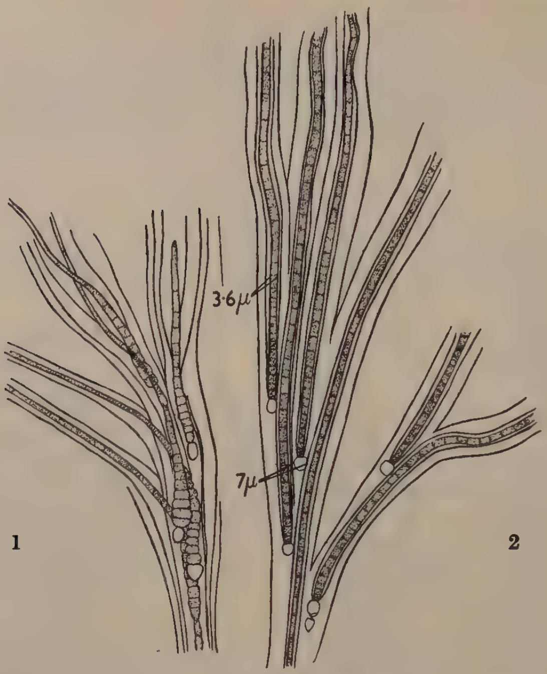

Fig. 13. 1, *Dichothrix gypsophila* (After Engler and Prantl.); 2, *Rivularia vieillardii* (Original).

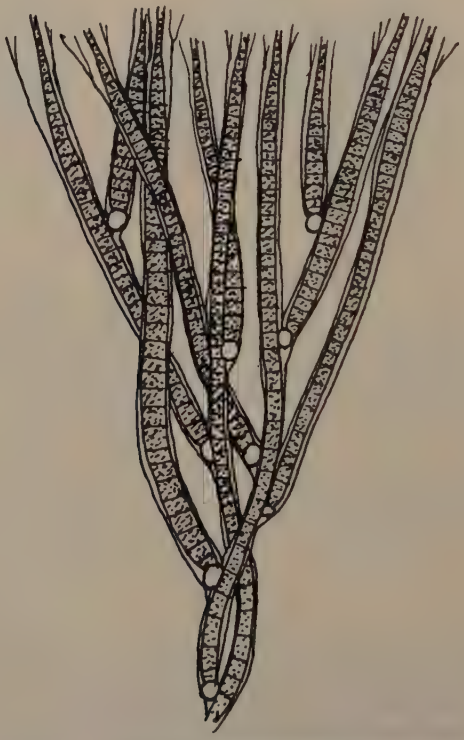

Fig. 14. *Rivularia atra.*

5–6·2μ and terminating in a narrow hair; cross-walls indistinct below; sheath hyaline, inconspicuous; heterocysts basal, 7–10μ dia. (Fig. 14.)

DISTRIBUTION. Local: Piha, rocks with fresh water dripping from above. General: cosmopolitan.

(2) *Rivularia australis* Harv.

Harvey, *Trans. R. Irish Acad.* **22**, 566, 1854; Newton, *Handb. Brit. Seaw.*, p. 40, 1931; Laing, *Trans. N.Z. Inst.* **57**, 131, 1926.

Thallus irregular, globose, soft, hollow, usually metallic blue-green in colour; trichomes easily separated by pressure, long, almost parallel, expanding in width from 1–3μ near heterocyst to 5–7·5μ in meristematic region, then tapering to a fine hair; heterocysts 7–11 by 10–14μ; sheath only detectable near heterocyst. (Fig. 4, no. 1.)

DISTRIBUTION. Local: common on salt marshes; on wood, Russell, Matauhi Bay; on *Lichina*, Waiwera, Whangaparaoa, Gt. Barrier; on rocks, Kaikoura, Kaha Pt., Warrington, Portobello, Watering Bay. General: France, England, Australia and New Zealand.

(3) *Rivularia polyotis* (Ag.) Born. & Flah.

Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **4**, 360, 1886; Womersley, *Trans. R. Soc. S.Aust.* **70**, (2), 1946.

Colonies up to 8 cm. dia., at first hemispherical, pulvinate, finally becoming bullate, hollow, soft, light to dull blackish green; sheaths wide, lamellose, ocreate, funnel-shaped, the outer layers confluent, becoming yellowish brown with age; trichomes easily separated by pressure, 2–5μ dia. below, 8–14μ above, tapering into a short hair; lower cells twice as long as broad, upper cells twice as short as broad; heterocysts basal, ovoid to spherical, 10–18μ dia. (Fig. 12, nos. 2, 3.)

DISTRIBUTION. Local: upper littoral at Stanmore Bay, Orewa, Te Haruhi Bay. General: Europe, Atlantic, Mediterranean, South Australia.

(4) *Rivularia vieillardii* (Kütz.) Born. & Flah.

Geitler, in Pascher's *Süsswass. Fl.* **12**, 240, 1925.

Colony irregularly lobed, up to 3 cm. broad, 1 cm. high, gelatinous, elastic, solid, olive-black in colour; threads lax, separating under pressure; sheath broad, lamellose, ocreate, dilating to tip, outer lamellae confluent with gelatinous matrix; trichomes 7–9μ thick, yellowish, terminating in a hair; lower cells constricted at joints, upper 3 times longer than broad. (Fig. 13, no. 2.)

DISTRIBUTION. Local: Frenchman's Creek, Anawhata, and probably elsewhere. General: New Caledonia.

Brachytrichia Zanard.

Colonies at first solid, finally hollow, composed of *Nostoc*-like filaments embedded in gelatine; filaments flexuously curved, parallel, tapering above to a hair, very much branched; sheaths distinct in growing filaments, tubular, finally becoming confluent and invisible; heterocysts intercalary.

Brachytrichia quoyi (Ag.) Born. & Flah.

Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **4**, 373, 1886.

Colonies up to 5 cm. dia., plicate-expanded and bullate, confluent, blackish green. (Fig. 15.)

DISTRIBUTION. Local: upper littoral rocks, Stanmore Bay. General: Massachusetts, New Jersey, California, South Australia.

Isactis Thuret

Plant mass flat, crustaceous, orbicular, thin, adhering by the lower surface, growing at the margin; filaments parallel, erect, unbranched or sparingly branched; heterocysts basal; gonidia unknown.

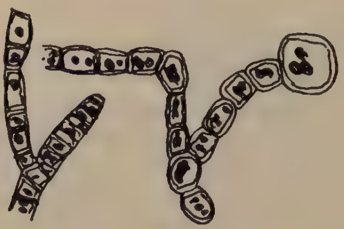

Fig. 15. *Brachytrichia quoyi* (after Gomont). (× 600.)

Isactis plana (Harv.) Thuret

Thuret, *Ann. Sci. Nat. Bot.* (6), **1**, 372, 1875; Born. & Flah., *Ann. Sci. Nat. Bot.* (7), **4**, 344, 1886.

Plant mass green, becoming brown or black; filaments prostrate at base, up to 0·5 mm. long; sheaths close, transparent, sometimes yellowish, scarcely distinct; trichomes 7–9μ dia., terminating in a long hair. (Fig. 4, no. 2.) V.W.L. 52.

Distribution. Local: Bay of Islands, Stanmore, Narrow Neck, Orewa, Arkles Bay, Cape Rodney, Arran, Little Barrier, Gt Barrier, Fletchers Bay, Pihama; common on rocky shores between H.W.N.T. and H.W.S.T. General: U.S.A.; South Australia.

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CHLOROPHYCEAE

These plants contain the same four pigments in the chlorophyll as are found in the higher plants, though their proportions may be different. The plant body varies from single uninucleate cells to complex colonies and multicellular plants which vary widely in form. These are either composed of uninucleate cells (Ulvaceae) or else are partially coenocytic (Siphonocladales). There are also simple and branched filaments and completely coenocytic forms (Siphonales). The cell walls vary in structure but are generally of cellulose, though pectose is not infrequent. The walls differ greatly in thickness, and in some genera may be heavily encrusted with lime. The chloroplasts are very varied in their shape and generally contain pyrenoids. Vegetative reproduction is a frequent phenomenon whilst asexual reproduction takes place by means of zoospores, akinetes or aplanospores. Sexual reproduction ranges from isogamy to oogamy, the plants being either monoecious or dioecious. In some genera there is a well-marked alternation of generations (*Ulva*, *Enteromorpha*, *Cladophora*, etc.).

Although a number of species of Chlorophyceae have been recorded in Laing's (1926) list, a study of his herbarium shows that it contains several additional species. Some genera (*Ulva*, *Enteromorpha*, *Bryopsis*) were recognized as requiring detailed study before any final conclusions could be reached. An attempt has been made to provide this detailed study and it has resulted in the appearance of a number of new species, some of them remarkable (e.g. *Gemina* spp.).

A study of the smaller forms has also resulted in the recording of several additional species not previously recorded for New Zealand and further new species.

In preparing this list I am grateful to Miss U. V. Dellow who undertook the genera *Microdictyon* and *Codium*.

Although some of the new species appear to have a very restricted distribution, further collecting will undoubtedly extend their range. Of the species described, no less than 92 are endemic. This is in marked contrast to the Myxophyceae.

It might be thought that the number of new species and forms is excessive. It must be borne in mind that the algal flora of New Zealand has not, as a whole, been critically studied. The same is also true of the algal flora of Australia. It is therefore not perhaps surprising to find a large number of new species. The rather better known flora of South America is rich in species and genera which do not occur elsewhere, and it is evident that the subantarctic and antarctic represents an area rich in endemic forms.

The arrangement of the families and orders follows that given in Fritsch (1935).

Type specimens are noted as located in one of the following herbaria: Auckland Institute, Mr V. W. Lindauer, Botany Division Herbarium (D.S.I.R. Wellington), Laing Collection (Canterbury University College).

KEY TO THE FAMILIES IN NEW ZEALAND

1.	Thallus consisting of a single cell.	Chlorococcaceae
	Thallus of more than one cell.	2
2.	Thallus wholly coenocytic.	3
	Thallus cellular or only partially coenocytic.	8
3.	Branched filaments, endophytic or endozoic.	Phyllosiphonaceae
	Thallus otherwise.	4
4.	Thallus with creeping rhizome, rhizoids and erect aerial forms.	Caulerpaceae
	Thallus otherwise.	5
5.	Thallus filamentous, filaments not interwoven.	6
	Thallus spongy, flabelliform, cylindrical or mat-like, consisting of interwoven filaments.	Codiaceae
6.	Plants tufted, branching radial or pinnate.	Bryopsidaceae
	Portion of thallus creeping with erect filaments, branching irregular or dichotomous.	7
7.	Reproduction by simple zoospores.	Derbesiaceae
	Reproduction by compound zoospores and oogamy	Vaucheriaceae*
8.	Thallus of unbranched, uniseriate filaments with banded chloroplast.	Ulotrichaceae
	Thallus more complex, or, if unbranched, cells with reticulate chloroplasts.	9
9.	Thallus membranous or tubular, multiseriate.	13
	Thallus filamentous, uniseriate, simple or branched.	10
10.	Branched microscopic filaments, often with hairs	Chaetophoraceae
	Macroscopic filaments without hairs.	11
11.	Mature thallus forming a net.	Microdictyaceae
	Mature thallus otherwise.	12
12.	Filaments simple or branched, septation not delayed.	Cladophoraceae
	Filaments simple, branched or vesicular, septation delayed.	Valoniaceae
13.	Thallus monostromatic.	14
	Thallus distromatic, tubular or composed of two rows of cells.	16
14.	Chloroplast parietal.	15
	Chloroplast axial.	Prasiolaceae
15.	Minute prostrate epiphytes (microscopic).	Chaetophoraceae
	Thallus larger.	Monostromaceae
16.	Thallus tubular, cells in areolae.	Capsosiphonaceae
	Thallus membranous or tubular, cells not in arveolae.	Ulvaceae

* This family is regarded as belonging to the Xanthophyceae.

CHLOROCOCCALES

Unicellular or colonial aggregates of non-motile cells. Number and shape of chloroplasts various; reproduction various; the plant is haploid, only the zygote is diploid.

Chlorococcaceae

Unicellular algae possessing a single chloroplast with one or more pyrenoids; reproduction by means of biciliate swarmers.

Codiolum A. Braun

Frond unicellular, ovoid to clavate or subcylindrical, the cell wall prolonged below into a longer or shorter stipe; chloroplast more or less filling the cell and containing several pyrenoids.

Codiolum kuckuckii Skottsb. & Levr.

Levring, *Nat. Hist. Juan. Fern.* 2, 604, fig. 1, 1941; Skottsberg, *Svensk. Bot. Tidskr.* **14**, 277, 1920.

Cells endophytic in *Splachnidium rugosum*, pyriform, with a long stipe, up to 90μ long, pyriform body 20–30μ long by 10–18μ wide, stipe filiform, more or less obtuse, apex thickened or completely solid. (Fig. 16*c*.)

Distribution. Local: Auckland and probably throughout host range. General: East Indies, Australia, Tasmania, Juan Fernandez, San Felix.

Although the host plant occurs in South Africa the parasite is apparently absent.

ULOTRICHALES

Plants predominantly filamentous. The plate-like (*Ulva*) and tubular (*Enteromorpha*) forms are regarded as elaborations of the filamentous type. Cell division septate, cells uninucleate in all marine forms: in some species there is alternation of generations. Some authorities segregate the membranaceous forms into a separate order, the Ulvales. Since the early stages of so many of these forms are akin to the Ulotrichaceous filament the present writer prefers to follow those authorities who include all these forms in the Ulotrichales.

1.	Plants consisting of simple, unbranched filaments	2
	Plants expanded or tubular, consisting of more than one row of cells.	3
2.	Chloroplast band-shaped.	Ulotrichaceae
	Chloroplast axial, radiating.	*Prasiola crispa* '*Hormidium*-stage'
3.	Thallus distromatic or tubular.	5
	Thallus monostromatic.	4
4.	Chloroplast parietal, lateral, plants usually large.	Monostromataceae
	Chloroplast axial, radiating, plants usually small.	Prasiolaceae
5.	Thallus tubular, cells in rows, the rows readily separating.	Capsosiphonaceae
	Thallus tubular or membranous, when cells in rows, the rows not separating.	Ulvaceae

Ulotrichaceae

Filaments simple, very rarely branched, usually attached to substratum by a specialized basal cell; cells in a series, uninucleate, with a complete or broken band-like chloroplast containing one to several pyrenoids; reproduction varied, zoospores 2–4-ciliate, gametes 2-ciliate.

Ulothrix Kütz.

Filaments simple, attached by a basal hold-fast cell, later sometimes free, walls thin to subgelatinous; cells with a parietal band-like plastid that more or less encircles the cell; quadriflagellate zoospores produced in all cells except the basal cell; sexual reproduction by biflagellate gametes.

The marine species of *Ulothrix* are not as well known as they should be. For this reason there are apparent wide discontinuities in distribution, though as our knowledge increases these gaps should become closed. It is likely that other marine species of *Ulothrix* occur around our shores.

1.	Cells usually as long as broad or almost so.	2
	Cells shorter than broad.	*U. flacca*
2.	Vegetative filaments 6–18μ dia.	*U. subflaccida*
	Vegetative filaments 25–28μ dia.	*U. novaezelandiae*

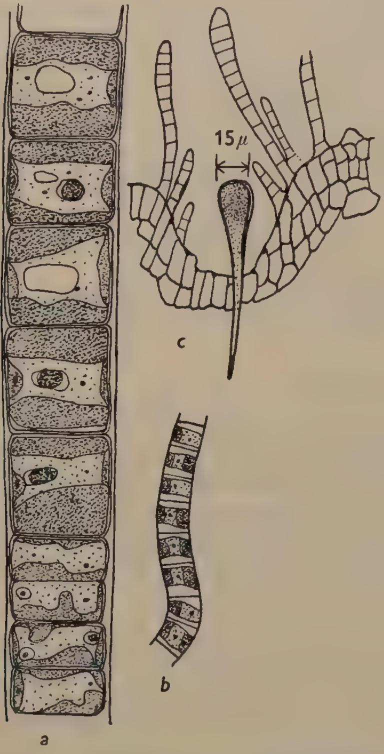

Fig. 16. *a*, *Ulothrix flacca*; *b*, *U. subflaccida* (after Carter); *c*, *Codiolum kuckuckii*.

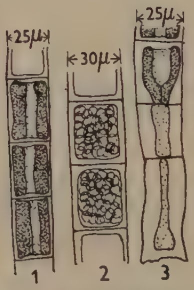

Fig. 17. *Ulothrix novae-zelandiae*: 1, vegetative cells; 2, reproductive cells; 3, attachment cell.

(1) *Ulothrix subflaccida* Wille

Taylor, *Mar. Alg. N.E. North Amer.* p. 47, 1937: Setchell & Gardner, Mar. Alg. Pac. Coast N. Amer., Chlorophyceae, p. 283, 1920 (as *U. implexa*).

Filaments tufted, 0·5–3 cm. long, entangled, attached or free-living; cells 6–18μ (average 10–15μ) dia.; 0·8–1·0 times as long as broad; chloroplast occupying only the middle part of the side wall of the cell; colour pale yellowish green. (Fig. 16*b*.)

Distribution. Local: Pihama, Godley Head, probably widely distributed. General: Florida, Canada, Europe, South Australia.

Chapman (1937) points out that *U. implexa* is the name given to a fresh-water species and that *U. subflaccida* is the corresponding marine species.

(2) *Ulothrix flacca* (Dillw.) Thur.

Taylor, *Mar. Alg. N.E. North Amer.* p. 46, 1938; Newton, *Handb. Brit. Seaw.* p. 56, 1931; Gain, Fl. Alg. Antarct. et Subant. p. 17, 1912.

Filaments entangled, 10–25μ dia., cells 0·25–0·75 times as long as broad; chloroplast occupying whole of cell; colour bright to dark green. (Fig. 16*a*.) V.W.L. 127 (*pro parte*).

Distribution. Local: Long beach, Arkles Bay, Port Fitzroy, Godley Head, St Clair, and probably elsewhere. General: New Jersey to Arctic, Europe, Mediterranean, Alaska to California, Kurile Is., Deception Island.

(3) **Ulothrix novaezelandiae** sp.nov.

Filamentis cristatis, brevibus, ad 3 mm. longis, per cellulam basalem immutatam adfixis, 25–28μ latis; cellulis quadratis vel aliquantum longioribus quam latioribus, cellula basali duplo longiore quam latiore; cellulis genitalibus 29–34μ dia., parietibus crassioribus; chloroplastio loriformi, cellulam totam occupante.[1]

Filaments tufted, short, up to 3 mm. long, attached by a modified basal cell, 25–28μ wide; cells quadratic or slightly longer than broad, basal cell twice as long as broad; reproductive cells 29–34μ dia., with thicker walls; chloroplast band-like, completely filling the cell. (Fig. 17.) Type specimen P.R.B.[2] no. 34,463, Cape Turakinae.

Distribution. Local: Cape Turakinae. Endemic.

This species differs from other known marine species. It is closely allied to *U. flacca* but the filaments are too narrow for it to belong to that species. The filaments are too wide for it to be *U. subflaccida* and also the cells are usually longer than broad.

MONOSTROMACEAE

Plants at first sac-like, usually soon splitting into a broad, flattened, segmented thallus one cell thick; chloroplasts single, parietal, with pyrenoids; reproduction by zoospores or gametes, the zygote enlarging before germination.

Monostroma is separated from *Ulva* and *Enteromorpha* and placed in a distinct family on the grounds of the difference in its life cycle. The other two genera both possess an alternation of generations which, so far as is known, is absent in *Monostroma*.

Monostroma Thuret

Plants at first saccate, usually splitting into broad, flattened blade or narrow segments one cell layer thick: cell walls thin or gelatinous, cells irregularly arranged or in groups; chloroplast single.

It is evident that a number of species occur in New Zealand. In many respects they resemble species described from elsewhere but they invariably differ in minor details. In some cases the variation is such as to suggest only varietal status, but in other cases it seems necessary to create new species.

1.	Plant retaining saccate shape for a long time.	2
	Plant soon splitting into expanded thallus.	3
2.	Plant 1 cm. or less in height, membrane 28–36μ thick.	*M. lindaueri*
	Plant rather larger, membrane 12–15μ thick.	*M. applanatum*
3.	Plant 1 cm. or less in diameter.	*M. parvum*
	Plant larger.	4
4.	Thallus more than 30μ thick.	5
	Thallus less than 30μ thick.	6
5.	Cells 6–8μ dia. in surface view.	*M. crepidinum* var. *pseudocrepidinum*
	Cells 11–15μ dia. in surface view.	*M. crepidinum*
6.	Thallus 15–26μ thick.	7
	Thallus 26–33μ thick.	*M. nitidum* var. *novae-zelandiae*
7.	Cells 5·5–8μ high in T.S.	*M. pacificum*
	Cells 9–11μ high in T.S.	8
	Cells 14–18μ high in T.S.	*M. latissimum*
8.	Thallus forming a very large expanded sheet up to 30 cm. long.	*M. latissimum* ecad *australis*
	Thallus smaller, not exceeding 14 cm. in length.	9
9.	Thallus deeply laciniate, margin not undulate.	*M. antarcticum*
	Thallus slightly laciniate, margin very undulate.	*M. moorei*

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[1] I am grateful to Mr L. W. Crawley for the Latin diagnoses.

[2] Botany Division Herbarium, D.S.I.R., Wellington.

(1) *Monostroma lindaueri* Chapman

Chapman, *J. Bot., Lond.*, **78**, p. 266, 1940.

Thallus, small, saccate, inflated, spherical or elongate, only rupturing very late; cells in young stage in rows horizontally and longitudinally, row arrangement indistinct in older thallus, cells 8–24μ dia., average 12–14μ; membrane 28–36μ broad, wall up to 3μ thick on the outside and up to 6–8μ on the inside. (Fig. 18.)

DISTRIBUTION. Local: Bay of Islands, Rangitoto; epiphytic or on stones. Endemic.

Since the first original description was given, further plants have been found in which it seems evident that the sac splits at a very late stage.

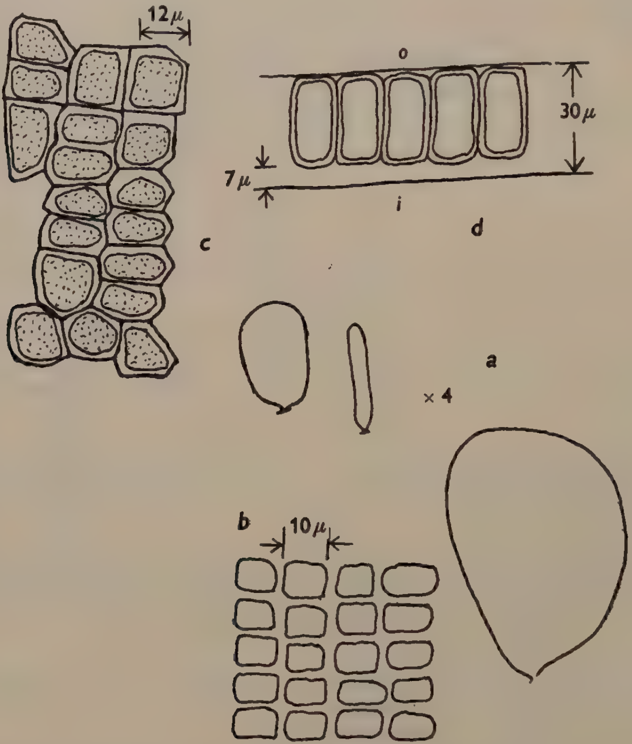

Fig. 18. *Monostroma lindaueri*: *a*, plants; *b*, cells in young part; *c*, cells in older parts; *d*, membrane.

(2) *Monostroma applanatum* Gain

Gain, Fl. Alg. Antarct. et Subant. p. 22, 1912.

Plant up to 2 cm. or more long, gradually attenuate to the base, open at the apex; cells irregularly arranged, 12–14μ dia.; membrane 12–15μ thick. (Fig. 20*a*.)

DISTRIBUTION. Local: Russell. General: Grahamland.

A single specimen in herb. Lindauer is placed here with some diffidence, especially since the measurements are not quite typical. *M. applanatum* is not a well-known species and was found growing epiphytically by Gain. Our plant has cells rather larger in transverse section. Further search should be made for the plant in New Zealand, especially in the South Island, with a view to determining its real nature. It is very closely allied to *M. harioti* Gain from which it differs in being thinner. (Fig. 20, *b*, *c*.)

(3) *Monostroma latissimum* (Kütz.) Wittr.

Wittrock, *Monostr.* p. 33, Tab. 1, fig. 4, 1866; Kütz., *Tab. Phyc.* **6**, tab. 14, 1856.

Plant attached at first, soon becoming free-floating; thallus soft, rounded or lobed, margin often undulate; in extent up to 3·0–4·5 cm. dia., cells in surface view irregularly arranged, 8–17μ dia., average 10μ; membrane 20–25μ thick, cells 14–18μ high in T.S. (Fig. 19.)

DISTRIBUTION. Local: Matauhi swamp, mangrove swamps (Auckland), creeks on Waiuku Road, Kaikorai lagoon and probably elsewhere. General: Bermuda, New England, Europe, Mediterranean, New Zealand.

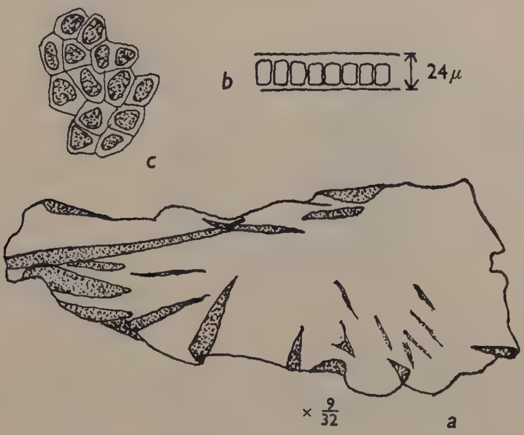

Fig. 19. *Monostroma latissimum*: *a*, plant; *b*, membrane; *c*, cells. (After Chapman.)

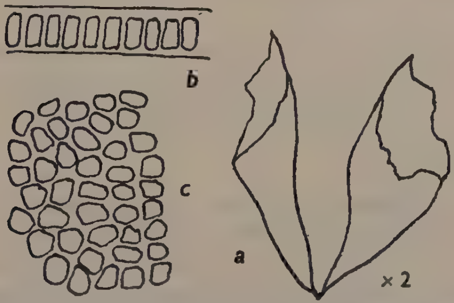

Fig. 20. *Monostroma applanatum*: *a*, plants. *Monostroma harioti*: *b*, membrane; *c*, cells. (*b*, *c*, after Levring.)

Monostroma latissimum ecad. **australis**. nov. ecad.

Thallo expanso, ad 30 cm. longo; membrana 22μ crassa, cellulis 11–12μ altis.

Forming large expanded sheets up to 30 cm. long; cells in surface view as in the parent species; membrane 22μ thick, cells 11–12μ high in T.S. (Fig. 21I, *a*, *b*.) P.R.B. no. 63,832 Waikanae.

DISTRIBUTION. Local: Waikanae estuary. Endemic.

This variety differs from the parent species in the somewhat smaller size of the cells in transverse section. They are definitely less than the values given by other workers for the species. This may be related to its particular habitat. For this reason it is treated as an ecad rather than as a variety.

(4) *Monostroma nitidum* var. **novaezelandiae** var.nov.

Thallo membranaceoso, adfixo, deinde libere fluitante, delicato et flaccido, gramino viridi, sublubrico, laciniato, marginis crispis et laceratis; membrana 26–33μ crassa; cellulis angulatis, subrotundis, 9–11μ dia., irregulariter dispositis, 9–11·5μ altis; chloroplastio cellulam totam occupante.

Thallus membranaceous, attached, later free-floating, delicate and flaccid, grass green, sublubricous, irregular, laciniate, margins crisped and lacerate; membrane 26–33μ thick, cells in surface view angular, subrotund, 9–11μ dia., usually irregularly arranged, in T.S. 9–11·5μ high; chloroplast occupying most of cell. (Fig. 21 II, *a*, *b*.) V.W.L. 3.[1] Type in herb. Auckland Inst. (Mick's Creek, Warkworth).

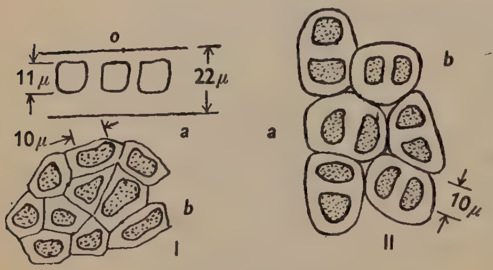

Fig. 21.

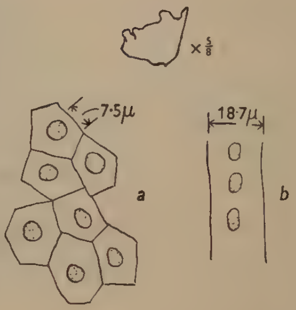

Fig. 22.

Fig. 21. I. *Monostroma latissimum* var. *australis*: *a*, membrane; *b*, cells. II. *Monostroma nitidum* var. *novaezelandiae*: *a*, cells; *b*, membrane.

Fig. 22. Above: *Monostroma parvum*. Below: *M. pacificum*: *a*, cells; *b*, membrane.

Distribution. Local: Uruiti, Orongo Bay, Warkworth, Hobson's Bay, Hooper's Inlet. Endemic.

This plant differs slightly in its measurements from the parent species but hardly enough to justify the creation of a new species. The membrane is up to 3μ thicker and the cells in T.S. are about 2μ shorter; the colour also is paler.

(5) **Monostroma parvum** sp.nov.

Planta parva, 1 cm. vel minus alta, adfixa, lubrica, pallido-viridi, delicata; membrana 18–20μ crassa, cellulis 5·5–8μ per sectionem altis, membranam mediam occupantibus; cellulis per planum visis angularibus, 11·5–15μ, irregulariter dispositis.

Plant small, 1 cm. or less in height, attached, lubricous, pale green, delicate; membrane 18–20μ thick, cells 5·5–8μ high in T.S., occupying the centre of the membrane; cells in surface view angular, 11·5–15μ, irregularly arranged. (Fig. 22.) Type specimen in herb. Auckland Inst., from Houhora.

Distribution. Local: on sand at Houhora at mouth of Waitangi stream, Bay of Islands, Leigh, Stanmore, Hobson's Bay, Narrow Neck, Te Haruhi Bay.

This species is characterized by its small size and very pale colour. In its cell measurements and thallus thickness it is very closely allied to *M. pacificum*.

(6) **Monostroma pacificum** sp.nov.

Thallo membranaceoso, adfixo, ad 12 cm. longo, lubrico, pallido-viridi, delicato; membrana 18–20μ crassa, cellulis 5·5–8μ altis, membrana utrimque crassata; cellulis per planum visis angularibus, irregulariter dispositis, 11·5–15μ dia.

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[1] Number of a specimen distributed by V. W. Lindauer in his Exsiccatae.

Thallus membranaceous, attached, up to 12 cm. long, lubricous, pale green, delicate; membrane 18–20μ thick, cells 5·5–8μ high, membrane thickened on both sides; cells angular in surface view, irregularly arranged, 11·5–15μ dia. (Fig. 22.) Type specimen No. 336 in herb. Laing (no locality on sheet).

DISTRIBUTION. Local: Manakau (Puketutu Is.), Tauranga, Wellington. Endemic.

This species differs from the preceding solely in size, but the difference is so marked that it cannot represent a growth phase of the former, especially since plants of both sizes have been collected at the same time of the year.

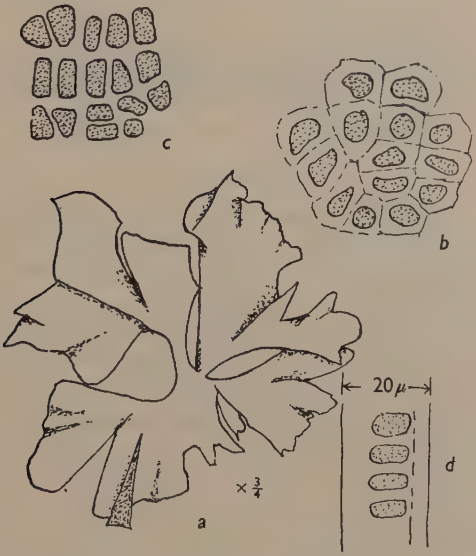

Fig. 23. *Monostroma antarcticum*: *a*, plant; *b*, *c*, cells; *d*, membrane.

(7) **Monostroma antarcticum** sp.nov.

Thallo membranaceoso, adfixo, ad 6 cm. dia., lubrico, pallido-viridi, alte in lobos laciniato; membrana 19–26μ crassa, cellulis 9–11μ per sectionem altis, 4–11·2μ dia., irregulariter vel obscure in pares, perraro in quaternas dispositis; chloroplastio cellulam totam occupante, materia intercellulari sat crassa.

Thallus membranaceous, attached, up to 6 cm. dia., lubricous, pale green, deeply laciniate into lobes; membrane 19–26μ thick, cells 9–11μ high in section, 4–11·2μ dia., arranged irregularly or obscurely in pairs, very rarely in fours; chloroplast occupying all the cell, intercellular material moderately thick. (Fig. 23.) Type specimen in herb. Auckland Inst. from Matauhi Bay (Russell).

DISTRIBUTION. Local: Russell, Tauranga, Stewart Is., and probably elsewhere. Endemic.

This species is near to *M. latissimum* but differs in the smaller size of the cells in transverse section. It is also close to *M. moorei* from which it differs in the deep segmentation.

(8) **Monostroma moorei** sp.nov.

Thallo membranaceoso, pallide gramino-viridi, adfixo, late orbiculato, ad 14 cm. dia., margine aliquantum laciniato, partibus extremis valde undulatis, membrana 24–25μ crassa, cellulis 9·3μ altis, membrana utrimque crassata; cellulis 8–11·5μ dia. per planum visis, irregulariter dispositis, materia intercellulari crassa.

Thallus membranaceous, pale grass-green, attached, broadly orbiculate, up to 14 cm. dia., the margin slightly laciniate, the edges much undulated, membrane 24–25μ thick, cells 9·3μ high, membrane thickened on both sides: cells 8–11·5μ dia. in surface view, irregularly arranged, intercellular material thick. (Fig. 24.) Type specimen in P.R.B. no. 55,834, from Collingwood.

Distribution. Local: Collingwood. Endemic.

This species is very similar to *M. antarcticum* but differs in the brighter green of its colour and the very undulate margin which is not so deeply laciniate as in *M. antarcticum*. This species is named after Miss L. B. Moore who discovered it.

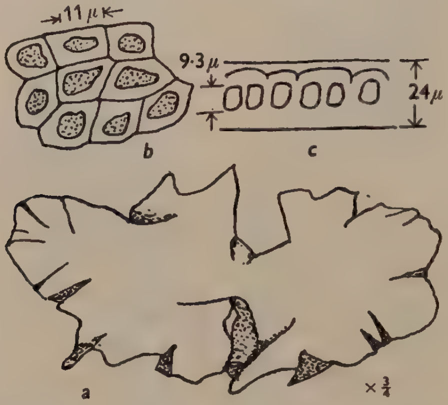

Fig. 24. *Monostroma moorei*: *a*, plant; *b*, cells; *c*, membrane.

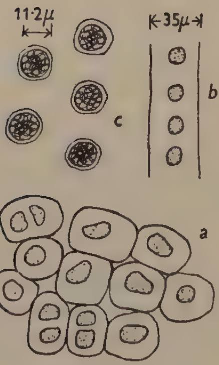

Fig. 25.

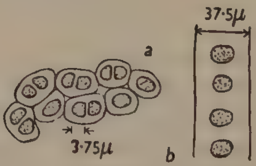

Fig. 26.

Fig. 25. *Monostroma crepidinum*: *a*, vegetative thallus; *b*, membrane; *c*, reproductive thallus.

Fig. 26. *Monostroma crepidinum* var. *pseudocrepidinum*: *a*, cells; *b*, membrane.

(9) *Monostroma crepidinum* Farlow

Farlow, Algae New England, *Rep. U.S. Fish Comm.* 1879, p. 42, 1881.

Thallus delicate, light green, 2·5–15 cm. long, flabellately-orbiculate, split to the base when fully developed, laciniae obovate; membrane 18–36μ thick; cells roundish angular, 11–15μ dia., 11·2μ high in T.S., when actively dividing forming groups of 2, 3 or 4, separated by wide spaces. (Fig. 25.)

Distribution. Local: Frenchman's Creek, Rangitoto. General: England, Boreal East America.

(10) *Monostroma crepidinum* var. **pseudocrepidinum** var.nov.

Thallo delicato, pallido-viridi, 2·5–8 cm. dia., alte caeso, laciniis obovatis, membrana 37–39μ lata; cellulis rotundo-angulatis, in pares ubi naviter dividuntur dispositis, 6–8μ dia., 11·2μ altis in T.S., regionibus intercellularibus arctioribus quam in *M. crepidino.*

Thallus delicate, pale green, 2·5–8 cm. dia., deeply cut, laciniae obovate, membrane 37–39μ wide; cells rotundo-angulate, in pairs when actively dividing, 6–8μ dia., 11·2μ high in T.S., intercellular zones not so wide as in *M. crepidinum.* (Fig. 26.) Type specimen in herb. Chapm. from Orongo Bay.

Distribution. Local: streams in mangrove swamp, Orongo Bay (Bay of Islands). Endemic.

This variety differs from the species in the slightly greater thickness of thallus, in the smaller size of the cells as seen in surface view and in the rather closer spacing of the cells.

ULVACEAE

Plants filamentous or foliaceous, tubular or membranaceous, membrane composed of two layers of cells; attached or becoming free-floating; plastids one or two, lateral, with a single pyrenoid; reproductive cells unaltered or slightly enlarged.

Letterstedtia as originally described is typified by *L. petiolata.* This species in its extreme form looks very unlike an *Ulva*, but there are forms with wide bases that look somewhat like *U. lobata*, and the variations in size of cells in *U. lobata* show that it has affinities with *Letterstedtia.* It differs, however, in the absence of the stipe interstitial cells. *L. ulvoidea*, on the other hand, has the appearance of an *Ulva* but does possess the interstitial cells in the stipe region. It would seem therefore that the presence of these interstitial cells is the only valid character separating these forms from species of *Ulva.* The discovery of *Lobata foliosa* and *L. phyllosa* has complicated the issue still further, because these plants have the appearance of *Ulva linza*, but the microscopic structure of a *Letterstedtia.* They are also probably anomalous in their mode of reproduction, so that, pending culture experiments they have been removed into a new genus. The discovery of the genus *Gemina* also provides a link between *Ulva*, *Enteromorpha* and *Capsosiphon.* These discoveries may mean that the only satisfactory treatment of these groups is to regard them as forming one genus divided into a number of subgenera.

1.	Adult plants tubular in cross-section.	2
	Adult plants of two rows of cells.	*Enteromorpha percursa*
	Adult plants forming a flat, distromatic plate.	3
2.	Cells arranged in distinct pairs.	*Gemina* (in part)
	Cells otherwise arranged.	*Enteromorpha*
3.	Cells arranged in distinct pairs.	*Gemina* (in part)
	Cells otherwise arranged.	4
4.	Thallus with a long narrow stipe, branching, with expanded leafy portion.	*Letterstedtia*
	Thallus with short stipe, or if elongate, not branching.	5
5.	Reproductive bodies formed from any cell except those of stipe.	*Ulva*
	Reproductive bodies formed in certain cells only of central region.	*Lobata*

Letterstedtia J. Ag.

Thallus flat, membranaceous, distromatic; stipe linear, taeniform-elongate, branched variously, branches expanding to leafy appendages, oblong or cuneate-lobed; reproduction by zoospores from expanded portion.

1.	Cells 1–2 times as long as wide in section.	*L. ulvoidea*
	Cells 2–2½ times as long as wide in section.	*L. stipita*
	Cells 2½–3 times as long as wide in section.	*L. petiolata*

(1) *Letterstedtia petiolata* J. Ag. (=*Phycoseris paradoxa* Grün.)

J. Ag., *Till. Alg. Syst.* **6**, 176, tab. 4, figs. 123–4, 1882.

Young thallus sessile, lamina more or less expanded, deeply laciniate, lacinia linear below, gradually broadening above, subpinnatifid; adult thallus with a stipe, lower part with varied branching, branches expanding to a leafy blade, cuneate-lobed, cells irregularly arranged, 7·5–11μ dia., 25μ high in T.S.; membrane of expanded part 52μ wide, scarcely thickened, of stipe 90μ wide, thickened on the outside, the two layers of cells separated by internal subsidiary cells; olive green or greenish brown in colour; may or may not adhere to paper. (Fig. 27; Pl. 24.)

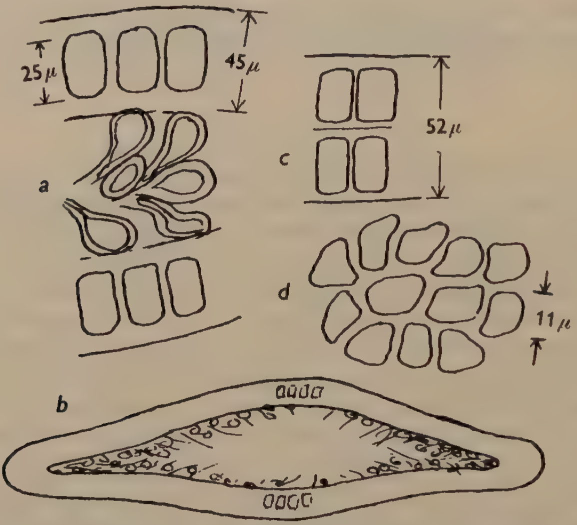

Fig. 27. *Letterstedtia petiolata*: *a*, T.S. stipe region; *b*, ditto; *c*, membrane of flattened portion; *d*, cells of flattened blade.

Distribution. Local: Bluff (90-Mile Beach), Russell, Cape Brett, Hokianga, Ti Titoki, Piha, Bethell's, Little Barrier, Oruawharo Bay, Mokohinau Is., Thames, Kawhia, Oaro, Te Araroa, Little Wanganui River, Levin, Dusky Sound, Campbell Is., Enderby Is. General: Australasia, East Indies.

In the typical form (Pl. 24) this species is readily recognizable, but smaller plants may be confused with the second species unless sections are cut. The thickness of the membrane increases from the lobes to the stipe, and in the stipe there are the characteristic secondary cells figured by Agardh. In young plants the expanded lobes are usually entire, but in old plants the edge tends to become torn and ragged.

(2) *Letterstedtia stipita* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 47, 1952.

Thallus stipitate, stipe short to long, developing into an expanded cuneate lobe, stipe rarely simple, more often branched; plants up to 5 cm. long and 5 cm. wide, expanded portion often lacerate; cells irregularly arranged, 13–15μ dia., 33–38μ high in T.S.; membrane of expanded part 86–100μ wide, 5μ thick on the outside; plants brownish olive green, not adhering to paper. (Fig. 28.)

Distribution. Local: St Clair, Otago Harbour, Campbell Is., White Is. General: Java.

In the typical form this species is quite distinct from *L. petiolata*, but in some states the only means of distinguishing it is to measure the cells and the membrane. A specimen in Leiden Herbarium (Herb. Lug. Bot. 943, 82/16) collected by Suringar and labelled *Ulva fasciata* f. *letterstedtiana* belongs to this species.

(3) *Letterstedtia ulvoidea* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 48, 1952.

Thallus briefly stipitate, forming a flat central sheet from which lobed expansions arise from an attenuate base; central sheet perforate, lobes orbicular, entire plant up to 20 cm. dia.; cells 11–19μ (13–15μ average) dia., sometimes in short rows, 15μ high in the lobes, 27–30μ high in narrower basal portion, the two layers of cells in the basal portion separated by interstitial cells with thick walls; membrane 38μ wide in lobes, walls unthickened, 76–80μ wide in base with walls thickened; grass-green in colour, adheres well to paper. (Fig. 29.)

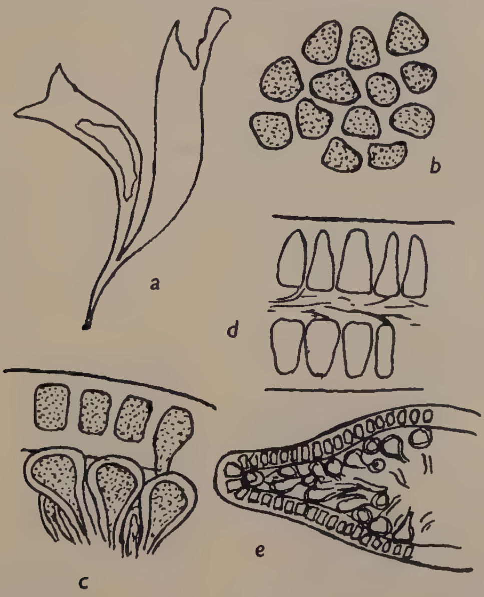

Fig. 28. *Letterstedtia stipita*: *a*, plant; *b*, cells of blade; *c*, membrane of stipe region; *d*, membrane of blade; *e*, T.S. stipe region.

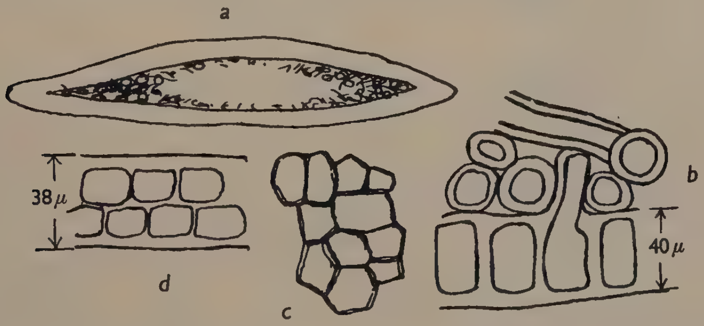

Fig. 29. *Letterstedtia ulvoidea*: *a*, T.S. stipe; *b*, membrane of stipe region; *c*, cells of blade; *d*, membrane of blade.

Distribution. Local: Kohaihai, Dusky Sound. Endemic.

This species combines the habit of an *Ulva* with the microscopic structure of a *Letterstedtia*. It is evident that the demarcation between the two genera is somewhat obscure. If the structure of the petiolar portion is regarded as a characteristic feature of *Letterstedtia*, then this plant, although more like an *Ulva* in appearance, must be classed as a *Letterstedtia*.

Ulva L.

Frond membranaceous, flat, consisting of two layers of cells usually closely applied throughout, but in some species separating at the base and margins; zoospores and gametes formed from any cell except those of the thickened or hollow stipe.

Key to the local species

1.	Thallus 2 cm. or less, *Enteromorpha*-like or expanding.	*U. parva*
	Thallus larger.	**2**
2.	Thallus narrow, linear, simple or branched.	**3**
	Thallus broad or variously dissected.	**5**
3.	Stipe long, hollow, cells 2 times as high as broad.	*U. linza*
	Stipe short, solid, cells 1½ or 3 times as high as broad.	**4**
4.	Cells 1½ times as high as broad, average dia. 13μ.	*U. brevistipita*
	Cells 3 times as high as broad, average dia. 8μ.	*U. taeniata*
5.	Adult thallus a broad, flat, expanded sheet	**6**
	Adult thallus lobed or dissected.	**10**
6.	Membrane less than 40μ thick.	*U. sorensenii*
	Membrane more than 40μ thick.	**7**
7.	Thallus bullose, cells 15–23μ high.	*U. laingii*
	Thallus plane, cells more than 22μ high.	**8**
8.	Cells 30–33μ high, 3 times as high as wide.	**9**
	Cells 26–28μ high, 2½ times as high as wide.	*U. latissima*
9.	Margin smooth.	*U. geminoidea*
	Margin heavily dentate.	*U. geminoidea* var. *dentata*
10.	Membrane of expanded part over 100μ.	**11**
	Membrane of expanded part under 100μ.	**13**
11.	Membrane 140μ, lobes few, very broad.	*U. crassa*
	Membrane 100–125μ, lobes narrower.	**12**
12.	Cells rounded in surface view.	*U. dactylifera* var. *rotunda*
	Cells angular in surface view.	*U. dactylifera*
13.	Cells less than 12μ high.	*U. fasciata*
	Cells more than 15μ high.	**14**
14.	Thallus deeply lobed, lobes cuneate.	*U. lobata*
	Thallus otherwise dissected.	**15**
15.	Cells more than 24μ high.	**16**
	Cells about 18μ high.	**18**
16.	Membrane 50–60μ thick, thallus entire.	*U. laetevirens*
	Membrane more than 60μ thick, thallus perforate.	**17**
17.	Margin heavily dentate.	*U. geminoidea* var. *dentata*
	Margin smooth.	*U. reticulata*
18.	Membrane 30–40μ, lacinulate and dentate.	*U. lactuca* var. *lacinulata*
	Membrane more than 40μ.	**19**
19.	Membrane 50–80μ, cells quadratic.	*U. lactuca* var. *rigida*
	Membrane 40–50μ, cells slightly longer than broad.	
20.	Plant grass-green.	*U. lactuca*
	Plant olive-green, restricted to Antarctic Islands.	*U. lactuca* var. *aucklandica*

(1) *Ulva linza* L.

Setchell & Gardner, Mar. Alg. Pac. Coast N. Amer., Chlorophyceae, p. 263, 1920; J. Ag., *Till Alg. Syst.* 6, 134, pl. 4, figs. 110–12, 1882; Laing, *Trans. N.Z. Inst.* 57, 135, 1926, as *Enteromorpha linza*; De Toni & Forti, Alg. Aust. Tasm. e Nuova Zel. p. 86, 1923 as *E. linza*.

Frond lanceolate or linear-lanceolate, simple, 1–5 dm. long, 1–20 cm. broad; stipe variable, hollow; upper part of frond flat, the two layers of cells completely united or remaining free along the whole or part of the margins, which are plane or more or less undulate; membrane 50–70μ thick; cells vertically elongate in section, usually about 2 times as long as broad. (Fig. 30.)

Distribution. Local: Piha, Anawhata, Seatoun, Island Bay, Brighton, Portobello Bluff, Stewart Is. General: Europe, Mediterranean, South Atlantic, West Indies, Tasmania, Peru, Alaska to Mexico, Kamchatka, China, Japan, Kurile Is.

Two forms of this species are sometimes distinguished, f. *lanceolata* with margins plane or undulate, and f. *crispata* with margins crisped. Since neither of these forms appears to be 'clear cut' I have followed Setchell and Gardner in omitting them. The species is not common in New Zealand, but in the past workers have placed other forms (e.g. *U. brevistipita*, *U. taeniata*, *Lobata phyllosa*, *L. foliosa*) under this species.

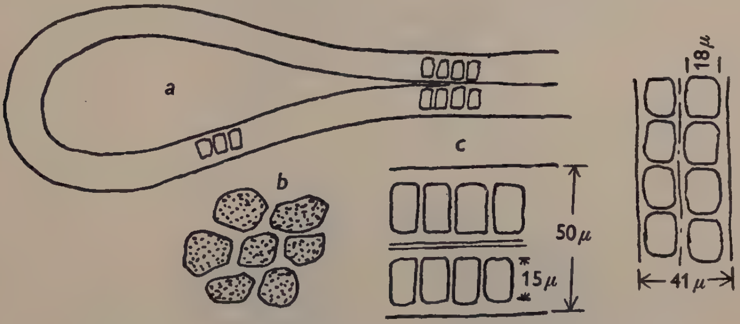

Fig. 30. *a–c*, *Ulva linza*: *a*, T.S. thallus; *b*, cells; *c*, membrane; *d*, *U. brevistipita*, membrane.

(2) **Ulva brevistipita** sp.nov.

Fronde adfixa, ovata-lanceolata, marginibus undulantibus, ad basim acute ad stipitem brevem attenuata; cellulis 11–18μ dia., 18–22μ altis in T.S.; membrana 41–60μ crassa, parietibus vix crassatis.

Frond attached, ovate-lanceolate, margins waved, attenuate sharply at the base to a short stipe; cells 11–18μ dia., 18–22μ high in T.S.; membrane 41–60μ thick, walls scarcely thickened; pale green in colour; usually adheres well to paper. (Fig. 30; Pl. 24.) Type specimen in Herb. Laing, from Titahi Bay.

Distribution. Local: Titahi Bay, Seatoun, Charteris Bay, Nelson, St Clair, Puketeraki, Taeri Beach, Stewart Is. Endemic.

In the past, this species has been mistaken for *U. linza* but it differs in the relationship between length and breadth (1¼ times) of the cells in T.S. and also in having a short, solid stipe.

(3) *Ulva taeniata* (Setch.) Setch. & Gardn.

Setchell & Gardner, Mar. Alg. Pac. Coast N. Amer., Chlorophyceae, p. 273, pl. 23, 1920.

Frond elongated, 1–2 m. long, simple or split to the very base into long, narrow segments, plane below and coarsely dentate, densely crisped and ruffled on the margins above, with a plane, thicker 'midrib'; membrane up to 140μ thick in 'midrib' region, but down to 40μ at the margins; cells of the 'midrib' vertically elongated in section to 3 times as long as wide, but nearly quadrate at the margins. (Fig. 31 I.)

Distribution. Local: Lyall Bay. General: Central California.

Two specimens collected on two different occasions from Lyall Bay agreed closely in all characters with an authentic specimen from California.

(4) *Ulva lactuca* L.

Collins, Green Alg. N. Amer. p. 214, fig. 75, 1909; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926.

Fronds short, usually broader than long, attached by a disk from a broad or attenuate base, generally deeply and irregularly split, delicate in texture, margins plane or ruffled; cells 11–15μ dia., 15–18μ high in T.S., almost quadratic; membrane 35–50μ thick, usually between 40 and 45μ, walls not thickened; light to dark green in colour; adheres well to paper. (Fig. 32 I.)

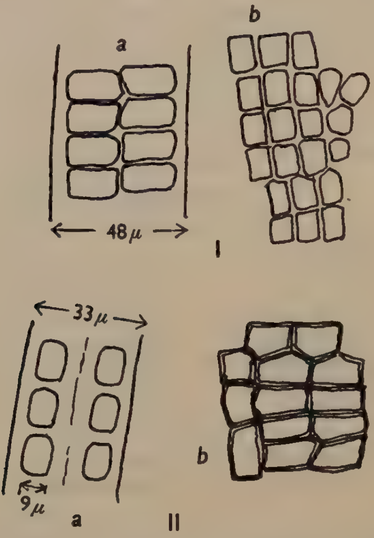

Fig. 31. I. *Ulva taeniata*: *a*, membrane near margin; *b*, cells. II. *U. fasciata*: *a*, membrane; *b*, cells.

Distribution. Local: Little Barrier Is., Gt Barrier Is., Rangitoto, Fletcher's Bay, Stanmore, Wellington (Seatoun, Lyall Bay, Wellington Heads), Lyttelton, Huia, Narrow Neck, Gough's Bay, Ahora Bay, Greymouth, Otago harbour, Stewart Is., Campbell Is., Chatham Is. General: widely distributed.

The plants belonging to this species are usually lighter in colour than var. *rigida* and the cells are slightly smaller in their measurements.

(5) *Ulva lactuca* var. *rigida* (Ag.) Le Jol.

Setchell & Gardner, Mar. Alg. Pac. Coast N. Amer., Chlorophyceae, p. 269, 1920; Kütz., *Tab. Phyc.* **6**, tab. 23, fig. 2, 1856; J. Ag., De Alg. Nov. Zel. Mar., p. 2, 1877 (*pro parte*); Harv. in Hooker, *Fl. Nov. Zel.* **2**, 265, 1855; *Handb. N.Z. Flora*, p. 715, 1867; Cotton, *Kew Bull. Misc. Inf.* **6**, 239, 1909; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926.

Frond lobed, at first lanceolate or ovate-lanceolate, firm and stiff with distinct stipe, later broader and irregularly deeply divided; cells 7·5–29μ, average 14–18μ dia., 18μ high in T.S., quadratic or rather longer than broad in section; membrane 52–80 (–110)μ wide, outer wall up to 6μ thick; light or dark green in colour; adheres imperfectly to paper. (Fig. 32 I.)

Distribution. Local: Kermadecs, Piha, Mahia, Tauranga, Wellington Heads, Moa Pt., Titahi Bay, Lyall Bay, Ohiro, Anatori River, Kaikoura, Lyttelton, Moeraki, Dunedin, Dusky Sound, George Sound, Bruce Bay, Blackhead, Chatham Is., Stewart Is., Snares, Auckland Is., Campbell Is. (?). General: North Atlantic, North and South Pacific, West Indies, Angola.

The record from Campbell Is. is included with some diffidence as the plant collected possessed a very unusually shaped frond, though the cell and membrane measurements were typical. The plant was cast up, and further search may show that it is a deep-water form which should be classed as a separate variety. The confines of this variety are not well determined (*vide* Setchell & Gardner) and the plants from New Zealand appear to have a rather thinner membrane than is usually found. They agree otherwise in characters with plants from other parts of the world.

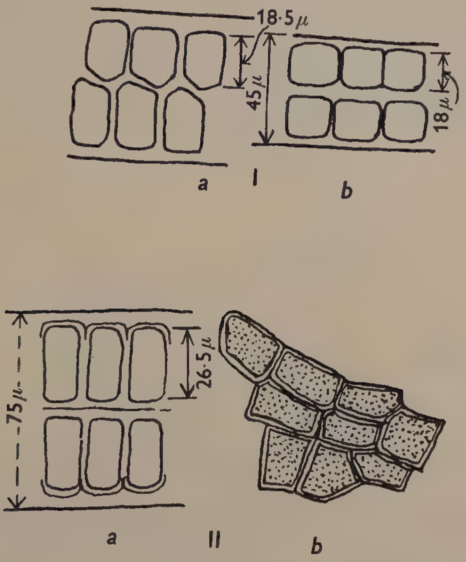

Fig. 32. I. *a*, *Ulva lactuca* var. *rigida*, membrane. I. *b*, *U. lactuca*, membrane. II. *U. latissima*: *a*, membrane; *b*, cells.

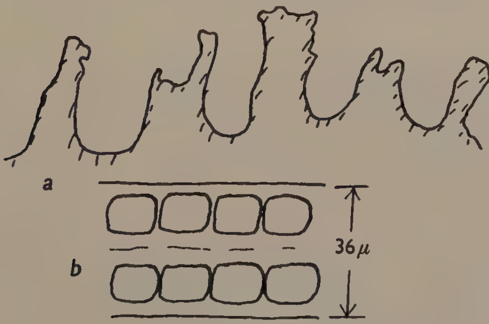

Fig. 33. *Ulva lactuca* var. *lacinulata*; *a*, edge of thallus; *b*, membrane.

(6) *Ulva lactuca* var. *lacinulata* (Kütz.) Hauck

Kütz., *Tab. Phyc.* 6, tab. 21, 1856; Feldmann, Alg. Mar. des Albères, *Rev. Alg.* 9, 195, fig. 10, 1937.

General shape of the frond as for the parent species, but the margin is irregularly dentate; cells 13–15μ dia., 12–15μ high in T.S.; membrane 30–40μ thick, walls slightly thickened; light or dark green in colour; adheres imperfectly to paper. (Fig. 33.)

Distribution. Local: Ahuriri Lagoon, Seatoun, Lyall Bay, Picton Lagoon, Waitati, Wycliffe Bay, Purakanui, Christchurch. General: Mediterranean.

Included here is probably the plant labelled f. *laciniata* (Wulf.) J. Ag., which De Toni (1889) records as present in New Zealand and described by Kützing as *Ulva australis*.

(7) *Ulva latissima* L.

Setchell & Gardner, Mar. Alg. Pac. Coast N. Amer., Chlorophyceae, p. 266, 1920; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877, as *U. rigida* (*pro parte*); Harv. in Hooker, *Fl. Nov. Zel.* **2**, 265, 1855; *Handb. N.Z. Flora*, p. 715, 1867; Harvey, *Phyc. Brit.* tab. 171, 1849–51; Cotton, *Kew Bull. Misc. Inf.* **6**, p. 239, 1909; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926.

Frond ample, broader than long, usually soon free and very much expanded, often reaching a considerable size; cells 7·5–22μ (average 14–16μ) dia., 26–28μ high in section; membrane (35–) 40–75μ thick, the outer wall up to 7μ thick, cells 2–3 times longer than broad in vertical section; yellow green in colour; adheres well to paper. (Fig. 32II.)

Distribution. Local: Poor Knights, Coromandel, Whitianga, Tauranga, Paremata, Happy Valley, Titahi Bay, Porirua, Tairoa Heads, Greymouth, MacAndrew Bay, Hoopers Inlet, Otago, Campbell Is., Stewart Is. General: all colder waters.

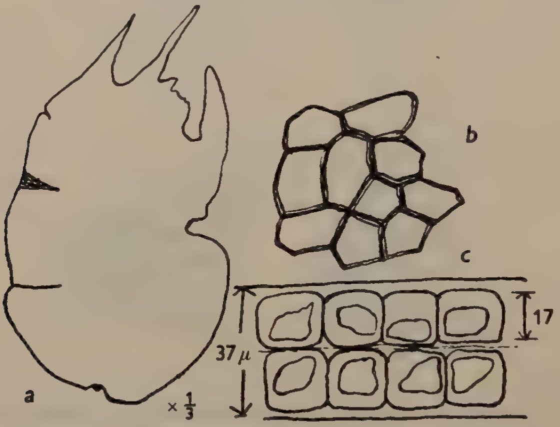

Fig. 34. *Ulva sorensenii*: *a*, plant; *b*, cells; *c*, membrane.

There is some doubt about the confines of this species. Plants labelled under this name from Europe have a much thicker membrane than is ascribed to it by Setchell and Gardner. The plants from New Zealand agree with the European plants in size, colour and width of membrane. In some cases the colour is darker, but that is possibly due to an excess of nitrogen in the local waters.

The only other large expanded form is *U. expansa*, and examination of an authentic specimen of this species shows that it differs from the New Zealand plants in that the cells are arranged in distinct rows and differ in length and breadth. The membrane, 52μ thick, is also thinner than that of the New Zealand plants and more nearly approaches that ascribed by Setchell and Gardner to *U. latissima*.

(8) **Ulva sorensenii** sp.nov.

Fronde ampla, lata, laminam magnam expansam formante, primum adfixa, novella ovali-lanceolata, maturiore irregulari et libera; cellulis 10–17μ dia., plerumque 13–14μ dia., 17μ altis in T.S.; membrana 37μ crassa, parietibus vix crassatis; colore pallide fulva-viridi.

Frond ample, broad, forming a large expanded sheet up to 30 × 17 cm., attached at first, oval-lanceolate when young, longer than broad, irregular and free when older; cells 10–17μ (average 13–14μ) dia., 17μ high in T.S.; membrane 37μ thick, walls scarcely thickened; colour pale brownish green; adheres well to paper. (Fig. 34.) Type specimen in Herb. P.R.B. No. 69,169, Campbell Is.

Distribution. Local: Stewart Is., Campbell Is., Auckland Is. Endemic.

According to Setchell and Gardner this plant would be placed in *U. latissima*. The appearance of the plant, the colour, and the form when young, are so distinctive as compared with plants distributed as *U. latissima* that it should clearly be regarded as a new species. It is a pleasure to name it after Mr J. H. Sorensen who has been responsible for collecting so many of these forms from the subantarctic islands.

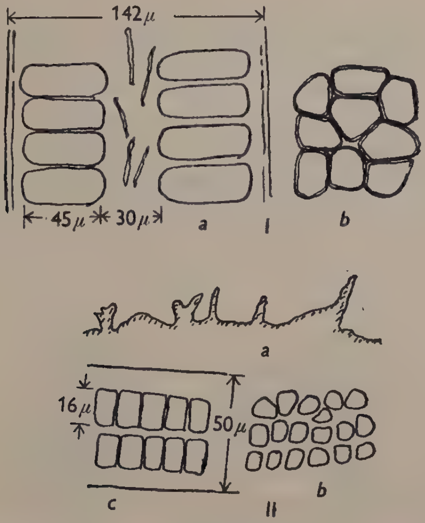

Fig. 35. I. *Ulva crassa*: *a*, membrane; *b*, cells. II. *U. laingii*: *a*, edge of thallus; *b*, cells; *c*, membrane.

(9) **Ulva crassa** sp.nov.

Fronde adulta in lobos latos interdum perforatos alte divisa, lobis late cuneatis, paulatim ad basim attenuatis, materia rigida; cellulis 15–26μ, plerumque 18μ dia., irregulariter dispositis, 45μ altis in T.S.; membrana 142μ crassa, pariete exteriore ad 6·5μ crasso, regione interstitiali ad 30μ crassa; colore oleagineo.

Mature frond deeply divided into broad lobes up to 20 cm. long and 14 cm. wide, entire or with occasional perforations, attenuate gradually to the base, substance stiff; cells 15–26μ (average 18μ) dia., irregularly arranged, 45μ high in T.S.; membrane 142μ thick, outer wall up to 6·5μ thick, middle zone up to 30μ thick; colour olive green; does not adhere to paper. (Fig. 35 I; Pl. 25.) Type specimen in Herb. V. W. Lindauer from Russell (Long Beach drift).

DISTRIBUTION. Local: Russell, Gisborne Dunedin. Endemic.

In general appearance the plant could be taken for *U. lactuca* or *U. lactuca* var. *rigida*, but it differs in its firmer substance and also in the great thickness of the membrane.

(10) **Ulva laingii** sp.nov.

Harv. in Hooker, *Fl. Nov. Zel.* **2**, 265, 1855; *Handb. N.Z. Flora*, p. 715, 1867 (both as *Ulva bullosa* Roth); ? Laing, *Trans. N.Z. Inst.* **57**, 135, 1926 (as *U. cornucopiae*).

Thallo formante laminas expansas ad 24 cm. longas, 17 cm. latas, bullosas, contortas, laceratas et scissas, margine dentato et lacinulato; cellulis 5·4–9·2μ, plerumque 7·5μ dia., 15–23μ altis in T.S., per ordines breves dispositis; membrana 48–65μ crassa, parietibus exterioribus valde crassatis; colore gramino-viridi.

Thallus forming expanded sheets up to 24 cm. long and 17 cm. wide, bullose, contorted, lacerated and torn, margin dentate and lacinulate; cells 5·4–9·2μ (average 7·5μ) dia., 15–23μ high in T.S., arranged in short rows; membrane 48–65μ thick, outer walls much thickened; grass green; does not adhere to paper. (Fig. 35 II; Pl. 26.) Type specimen in Herb. Laing, from mud flats, Heathcote.

DISTRIBUTION. Local: Collingwood estuary, Heathcote, Portobello, Otago Harbour, Porirua. Endemic.

In general appearance this species resembles *U. mesenteriformis*, but it tends to be larger in its dimensions. In view of the fact that *U. mesenteriformis* is described from Holland it is considered better to regard this as a new species. Mr Laing had sent a sheet to the late Prof. Setchell who said that he thought it was a form of *U. rigida*. The small size of the cells and the outer thickening of the membrane appear to demarcate it from *U. rigida*, and it seems better treated as a separate species. Experiments are, however, required in order to ascertain whether it is an ecological form, e.g. it occurs in places where the water may be stagnant or where there may be an influx of fresh water. Hooker records an *U. bullosa* from New Zealand, though no locality is given, and it is believed that his plants must belong to this species. It is also possible that Laing's (1926) *U. cornucopiae* belongs here, but no details are given in his list nor are there any specimens under this name in his herbarium.

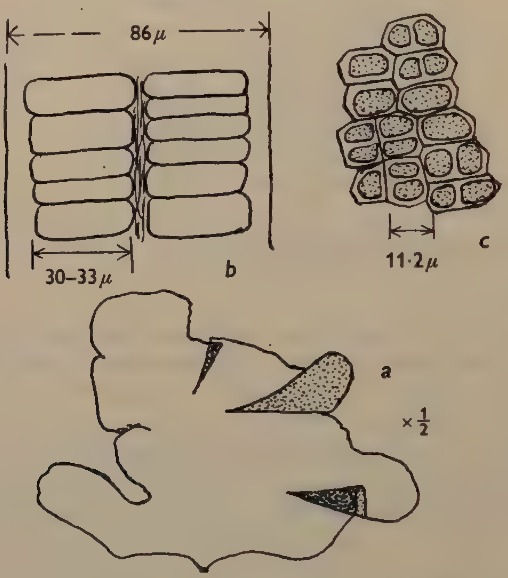

Fig. 36. *Ulva geminoidea*: *a*, plant; *b*, membrane; *c*, cells.

(11) **Ulva geminoidea** sp.nov. var. **geminoidea**

Fronde primum adfixa, breviter stipitata, late orbiculari, ad 20–23 cm. dia., vix divisa, deinde libere fluitante; cellulis 11–15μ dia., indistincte in pares et series dispositis, 30–33μ altis in T.S.; membrana 86μ lata, pariete exteriore ad 7·5μ crasso; colore fusco-viridi.

Frond attached at first, briefly stipitate, broadly orbicular, up to 20–23 cm. dia., scarcely divided, later becoming free-floating: cells 11–15μ dia., arranged indistinctly in pairs in rows, 30–33μ high in T.S.; membrane 86μ wide, outer wall up to 7·5μ thick; colour dark green; does not adhere well to paper. (Fig. 36.) Type specimen in Herb. P.R.B., no. 49,878, from Auckland Is.

DISTRIBUTION. Local: Russell, Anawhata, Tauranga, White Is., Moa Pt., Lyall Bay, Nelson, Kaikoura, Te Oka, Greymouth, Dunedin, Auckland Is. Endemic.

This species is characterized by the frequent paired arrangement of the cells, thus resembling the genus *Gemina*, but the cells are not conical in cross-section and the plant is clearly an *Ulva* rather than a *Gemina*.

(12) **Ulva geminoidea** var. **crispa** var.nov.

Fronde adfixa, elongata, ad 28 cm. longa et 10 cm. lata, margine valde undulatis; colore gramino-viride.

Frond attached, elongate, linear, up to 28 cm. long and 10 cm. wide, centre portion plane, margins folded and waved; measurements of cells and membrane as for the parent species; colour bright green; adheres well to paper. (Pl. 27.) Type in herb. Lindauer, from Bluff.

Distribution. Local: Bluff, Chalky Is., St Clair, Portobello, Port Elizabeth.

The habit of the plants is so distinct that it is considered they must form a separate variety.

(13) **Ulva geminoidea** var. **dentata** var.nov.

J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877 (as *U. rigida*, *pro parte*).

Fronde usque ad 6 cm. alta et 2 cm. lata, divisa, perforata, margine dentatissimo; cellulis in pares, 7·5–15μ, plerumque 11μ dia.

Frond attached, up to 6 cm. tall and 2 cm. wide, arising from a disk with a stipe, gradually expanding into a broad blade above, segmented, perforated and with numerous dentate prolongations on the margins; cells arranged mainly in pairs, 7·5–15μ (average 11μ) dia., 24–33·7μ high in section, rectangular or slightly conical; membrane 66–94μ thick, outer wall up to 7·5μ thick; colour dark green; does not adhere to paper. (Fig. 37; Pl. 28.) Type in Herb. Laing, no. 2469, from West Head.

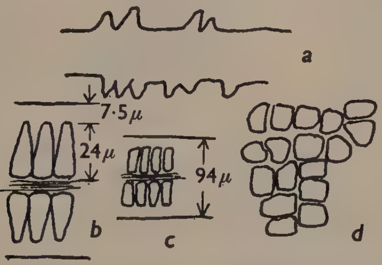

Fig. 37. *Ulva geminoidea* var. *dentata*: *a*, part of thallus; *b*, *c*, membrane; *d*, cells.

Distribution. Local: West Head, Lyall Bay, Breaker Bay, Banks Peninsula. Endemic.

This may prove to be an independent species, but for the present it is left as a variety of *U. geminoidea* to which it is obviously closely related. All specimens were very characteristic and there is no possibility of mistaking the variety. The specimen from the Banks Peninsula was collected by Berggren and identified by J. Agardh as *U. rigida*. The specimen in Agardh's herbarium is quite typical and agrees with the above description.

(14) *Ulva laetevirens* Aresch.

J. Ag., *Till Alg. Syst.* **6**, p. 167, 1882; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926.

Thallus up to 3 dm. or more long, deeply laciniate into a few segments, segments elongate, oblong to linear, margins undulate; cells irregularly arranged, 11–22·5μ (average 14–18μ) dia., 24–26μ high in section; membrane 50–60μ thick, walls scarcely thickened; colour yellow green; adheres well to paper. (Fig. 38I.)

Distribution. Local: Russell, Piha, Te Papa, Tauranga, Lyall Bay, Breaker Bay, Gore Bay, Picton, Akaroa, Lyttelton, Sumner, Black Head, Brighton, St Clair, Stewart Is. and probably elsewhere. General: Australia, Tasmania, and possibly subantarctic generally.

This is one of the common species, especially in the South Island. From a study of material in the University of Leiden I believe this species is synonymous with *Ulva* (*Phycoseris*) *gigantea* Kütz. from the Falkland Islands.

(15) *Ulva reticulata* Forsk.

J. Ag., *Till. Alg. Syst.* **6**, 166, 1882; Kütz., *Tab. Phyc.* **6**, tab. 29, 1856 (as *Phycoseris reticulata*); Hooker, *Handb. N.Z. Flora*, p. 715, 1867; Mont., *Voy. au Pole Sud., Bot. Crypt.* p. 33, 1842–45; Laing, *Trans. N.Z. Inst.* **57**, 136, 1926 (as *U. ligula*); De Toni & Forti, Alg. Aust. Tasm. e Nuova Zel. p. 84, 1923 (as *U. ligula*).

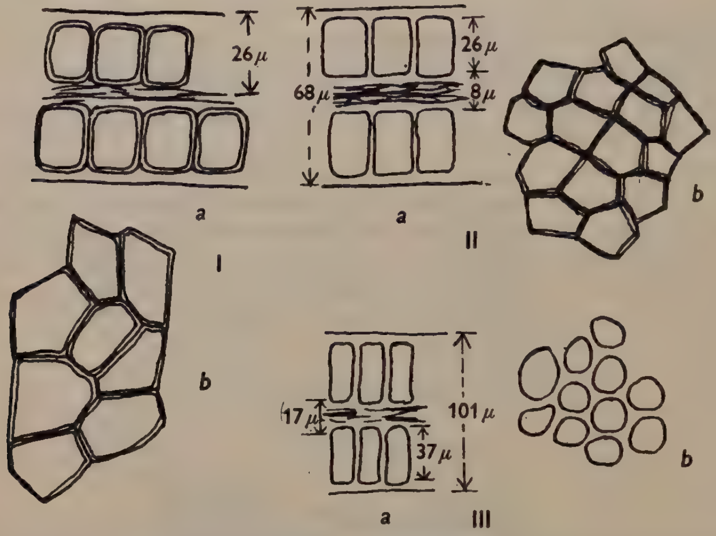

Fig. 38. I. *Ulva laetevirens*: *a*, membrane; *b*, cells. II. *U. reticulata*: *a*, membrane; *b*, cells. III. *U. dactylifera* var. *rotunda*: *a*, membrane; *b*, cells.

Frond arising from a stipe, expanding to a broad blade above, deeply laciniate, lower portions undulate and studded with rounded perforations, upper portions lacerated (perforations often confluent), perforations irregularly distributed, laciniae and perforations with a distinct cuticular margin; cells in short rows, 11–18μ, average 13–15μ dia., 26–32μ high in section; membrane 68–85μ thick, outer wall up to 4μ thick, central portion up to 8μ thick; light green in colour; adheres moderately to paper. (Fig. 38, II; Pl. 29.)

Distribution. Local: Piha, Waihi, Picton, Hokitika, Lyttelton, Riverton, Port Chalmers, Portobello, Chalky Inlet, St Clair, Auckland Is., Chatham Is. General: Red Sea, Ceylon, Tasmania, Philippines.

Hooker (1867) considers that Montagne recorded this species in error, but recent collections now indicate the latter was correct.

(16) *Ulva lobata* (Kütz.) Setch. & Gardn.

Setchell & Gardner, Mar. Alg. Pac. Coast N. Amer., Chlorophyceae, p. 268, 1920; Kütz., *Tab. Phyc.* **6**, 10, tab. 27, 1856 (as *Phycoseris lobata*).

Frond dark green, moderate in size, up to 30 cm. long and 15 cm. broad, more or less deeply lobed or divided, attenuate to acuneate, crisped, often more or less twisted at the base, margins plane or slightly undulate; membrane 44–112μ thick, thicker in the centre than at the margins; cells 11–18μ dia., 27μ high, vertically elongate, up to 2½ times as high as broad in the centre, nearly quadrate at the margins, sometimes arranged in short rows, grass green or olive green in colour; adheres moderately to paper. (Fig. 39II; Pl. 29.)

Distribution. Local: Bluff (90-Mile Beach), Bay of Islands, Piha, Tauranga, Pareoa, Lyall Bay, Kaha Pt., Greymouth, Bluff Hill. General: California, Chile.

A specimen in Kützing's herbarium at Leiden under this name from Yokohama appears to be more like *U. laetevirens*.

(17) *Ulva dactylifera* Setch. & Gardn.

Setchell & Gardner, Mar. Alg. Pac. Coast N. Amer., Chlorophyceae, p. 272, pl. 21, fig. 1, 1920.

Frond sessile or with a very short stipe; basal portion orbicular or reniform, much crisped, 2–4 cm. high, giving rise from the upper margin to 1–6 lanceolate, simple or occasionally branched lobes or laciniae with plane midrib and much crisped margins, 5–15 cm. high, 0·5–1·5 cm. wide; membrane of laciniae and basal portion 50μ thick at margin, up to 100μ in centre and up to 190μ in centre of laciniae; cells of basal portion 15–29μ (average 20–22μ) dia., of laciniae 10–18μ quadrate to 5 times as long as wide in section; colour grass green; adheres moderately to paper. (Fig. 39I.) V.W.L. 278.

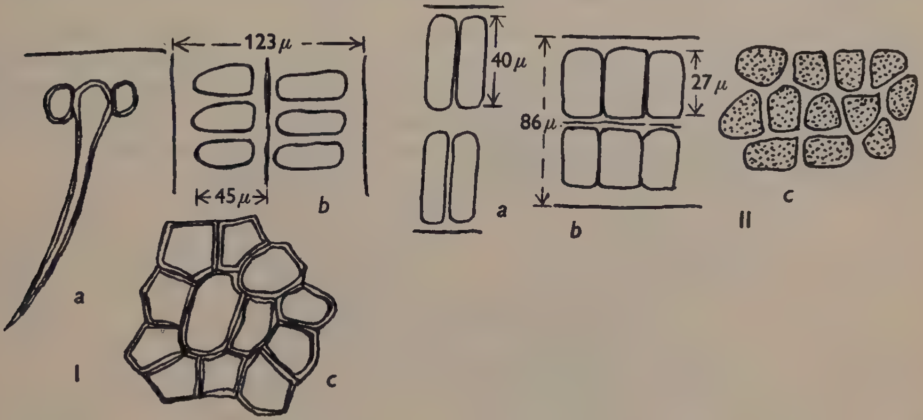

Fig. 39. I. *Ulva dactylifera*: *a*, long cell in centre of thallus; *b*, membrane; *c*, cells. II. *U. lobata*: *a*, membrane of central portion; *b*, membrane of lobe; *c*, cells.

Distribution. Local: Bluff (90-Mile Beach), Oeo, Anatori River, Greymouth, Stewart Is., Chatham Is. General: South California to Mexico and probably elsewhere in the Pacific.

This species is quite unmistakable and is allied to *Lobata phyllosa* and *L. foliosa* in its habit, but differs from them in possessing the basal portion from which the laciniae arise.

(18) *Ulva dactylifera* var. **rotunda** var.nov.

Cellulis rotundis, 9–13μ, plerumque 11μ dia., 37μ altis, parietibus intercellulis crassatis.

Plant attached, expanded, with lobes, up to 10 cm. high, slightly perforate; cells irregularly arranged, rounded, 9–13μ (average 11μ) dia., 37μ high in section with thick intercellular walls; membrane 100μ thick interstitial portion up to 17μ thick, traversed by extensions from the cells; pale green in colour; adheres well to paper. (Fig. 38III.) Type specimen P.R.B. 34,646, from Pt Nelson.

Distribution. Local: Port Nelson, Kaikoura.

The classification of these plants offered some difficulties. In some respects they appeared to be near to *U. delicata*, but the cells were not so high, and their rounded outline is characteristic; the interstitial portion is also much thicker. It differs from *U. dactylifera* in the cell shape and in size (the cells are smaller in diameter).

(19) *Ulva fasciata* Delile

Kütz., *Tab. Phyc.* **6**, tab. 28, 1856 (as *Phycoseris fasciata*).

Frond sessile or with a very short stipe, deeply laciniate almost to the base, laciniae narrow, lanceolate or expanding, margin not much crisped; cells arranged in indistinct rows, 11–18μ (average 13–15μ) dia., 8–11μ high in T.S.; membrane 33–37μ thick, outer walls thickened and with a distinct interstitial zone; colour grass green to bright green; adheres imperfectly to paper. (Fig. 31 II.)

DISTRIBUTION. Local: Karihana Bay, Warrington, Dusky Sound, Chatham Is. General: Mediterranean, Atlantic, Africa, Chile, Peru, Indian Ocean, West Indies.

(20) **Ulva parva** sp.nov.

Planta adfixa, epiphytica, stipitata, celeriter in partem latam vel linearem expansa, simplici vel laciniata, ad 2 cm. longa, 1·5 cm. lata; cellulis irregulariter dispositis, 5·5–15μ, plerumque 11μ dia., 5·5μ altis in T.S. in parte expansa; membrana partis expansae 16–17μ crassa, in regione basali multum crescente.

Plant attached, epiphytic, stipitate, expanding rapidly into a broad or linear portion, simple or laciniate, up to 2 cm. long and 1·5 cm. wide; cells irregularly arranged, 5·5–15μ (average 11μ) dia., 5·5μ high in T.S. in the expanded portion; membrane of expanded portion 16–17μ thick, increasing considerably in the basal region. (Fig. 40.) V.W.L. 228 (cotypes). Type specimen in Herb. Auckland Inst., from Russell (Long Beach).

DISTRIBUTION. Local: on *Corallina officinalis*, Russell, Hen and Chicken Is.

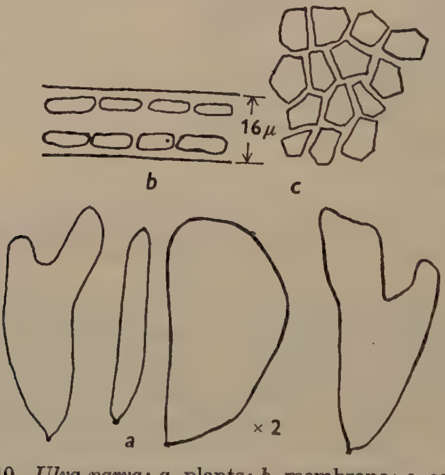

Fig. 40. *Ulva parva*: *a*, plants; *b*, membrane; *c*, cells.

This very small species is quite unmistakable, and Mr Lindauer informs me that it appears regularly and never reaches any greater size. This species is very close to *U. californica* and *U. uncialis* Sur. from both of which it differs in the thickness of the membrane (*U. californica* 30–50μ thick and *U. uncialis* 60μ thick in specimens examined), and the shape of the cells in section (flattened in *U. parva*, almost quadrate in *U. uncialis* and *U. californica*). It should not be confused with *Ulva parvula* Kütz. which appears to be a species of *Enteromorpha*. In thickness of the membrane it is close to *U. conglobata* Kjellm. from Japan but there is a difference in habit.

Lobata Chapm.

Frond elongate, with axis portion bearing lateral lobes, membranaceous, flat, consisting of two layers of cells, appressed in the marginal lobes, separated in axis: reproductive bodies produced in certain cells of axis portion.

The two species that at present are placed in this genus differ from *Ulva* and *Letterstedtia* in that the reproductive bodies appear to be confined to certain cells of the central axial portion. In *Ulva* and *Letterstedtia* any cell of the expanded portion can produce gametes or zoospores. The genus is allied to *Letterstedtia* in the presence of the lobed lateral appendages and the tendency for interstitial cells to develop in the axial region. What are believed to be the reproductive cells have so far only been seen in one of our two species, but the structure of the other is so similar that the two species are placed in the same genus with some degree of confidence. Since the finding of these two species another has been seen in the herbarium of the Allan Hancock Foundation in the University of S. California. Here also certain cells of the axial region appear to develop into reproductive cells.

1. Membrane of expanded lobes 54–65μ, cells 26μ high. *L. foliosa*
Membrane of expanded lobes 75–100μ, cells 30μ high. *L. phyllosa*

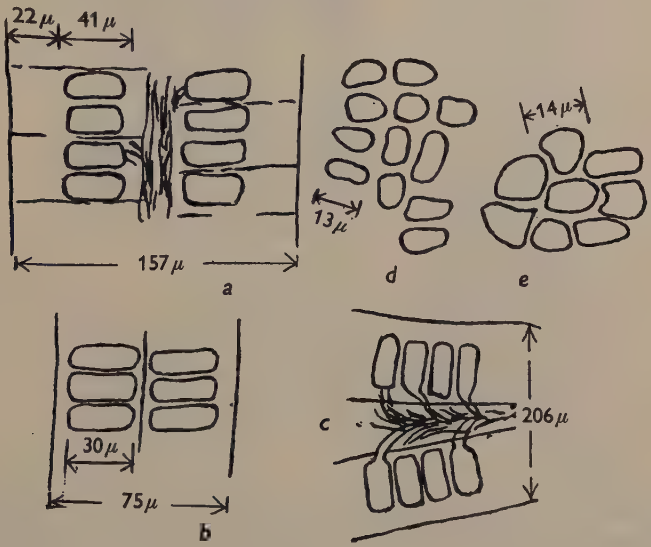

Fig. 41. *Lobata phyllosa*: *a*, *c*, membrane central region; *b*, membrane lateral portion; *d*, *e*, cells.

(1) *Lobata phyllosa* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 49, 1952.

Frond lanceolate or linear-lanceolate, simple or branched, up to 59 cm. long and 4 cm. wide, arising from a short stipe; upper part of frond consisting of a central axis-like portion, bearing broad, leafy, distichous lobes; cells of axis portion 13μ average dia., 41μ high in T.S. with prolongations into central region; cells of lobes 14–15μ average dia., 30μ high in T.S. without prolongations; membrane of lobes 75–100μ thick, outer wall up to 5μ thick; membrane of axis 150–206μ, outer wall up to 22μ thick; colour bright grass green; adheres well to paper. (Fig. 41.)

DISTRIBUTION. Local: Lyall Bay, Tauranga Bay, Timaru, Kowhaihai, Karamea, Chalky Inlet, Chatham Is. Endemic.

This species is very characteristic and can only be confused with *L. foliosa*, from which it differs in the brighter green colour, the greater length and narrower width, and in the greater thickness of the membrane. In so far as the axis portion differs from the lobes, the species is intermediate between *Ulva* and *Letterstedtia*.

(2) *Lobata foliosa* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 49, 1952.

Frond lanceolate or broadly linear-lanceolate, up to 30 cm. long and 8 cm. wide, sometimes branched from a more expanded basal portion, arising from a short stipe; branches consisting of a central axis portion bearing lobed appendages; cells of axis 5–11μ (average 8μ) dia., 26μ high in T.S.; cells of lobes 11–18μ, average 15–16μ dia., 26μ high in T.S.; membrane of lobes 54–65μ thick, walls scarcely thickened; membrane of axis 80–90μ thick, outer wall up to 11μ thick, occasional prolongations from cells into interstitial material; reproductive cells apparently restricted to axial region, swelling to 30μ; colour pale grass green; adheres moderately to paper. (Fig. 42; Pl. 30.)

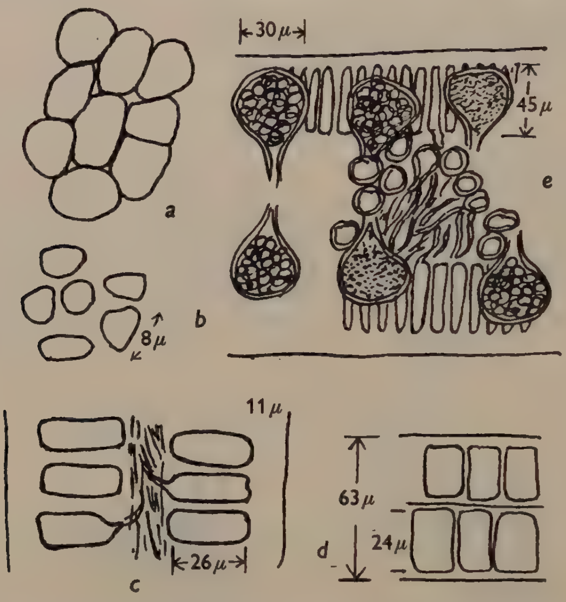

Fig. 42. *Lobata foliosa*: *a*, cells of lateral portion; *b*, cells of central portion; *c*, membrane of central portion; *d*, membrane of lateral portion; *e*, T.S. of central portion with reproductive cells

DISTRIBUTION. Local: Levin, Gore Bay, Wellington Heads, Karaka Bay, Lyall Bay, Waipapa boatshed, Tauranga Bay, Tautuku Bay, Timaru, St Clair, Portobello, Auckland Is., Chatham Is. Endemic.

One of the most interesting features of this species is the presence, as seen in one of the herbarium specimens, of large swollen cells in the axis portion. (Fig. 42*e*.) These cells contain rounded bodies and they represent the reproductive cells. If this is correct, we have here a species in which certain cells become modified for reproduction and are restricted to a portion of the thallus. Exactly similar cells were seen in a Californian specimen collected in the Gulf of California. Recently fresh material from Dunedin has been studied and similar enlarged cells liberated swarmers which did not fuse, nor did they develop after settling. They were considered to be gametes of one sex.

Gemina Chapm.

Thallus filamentous or foliaceous, distromatic, with or without a stipe; cells in pairs within the parent membrane, less frequently in threes or fours, long, narrow and conical in transverse section; reproduction (*G. linzoidea*) by swarmers produced in enlarged cells scattered through basal part of the thallus.

This is a remarkable genus because it combines the characters of *Enteromorpha*, *Ulva* and *Capsosiphon*. The species are all characterized by the regular paired arrangement of the cells, the pairs commonly being themselves arranged in short rows. *Gemina enteromorphoidea* has the exact appearance of an *Enteromorpha* whilst *Gemina ulvoidea* looks like a species of *Ulva*. In the cell arrangement the genus agrees with *Capsosiphon* but the thallus is never tubular, always distromatic, and there are no areolae. In possessing isolated reproductive cells it is similar to the genus *Lobata*.

1.	Thallus forming a broad expanded plate with or without a stipe.	4
	Thallus otherwise.	2
2.	Thallus long, linear, branched.	*G. enteromorphoidea*
	Thallus otherwise.	3
3.	Plant small, clavate.	*G. clavata*
	Plant larger, forming a cuneate blade.	*G. letterstedtioidea*
4.	Thallus without a stipe.	*G. ulvoidea*
	Thallus tapering to a long stipe.	*G. linzoidea*

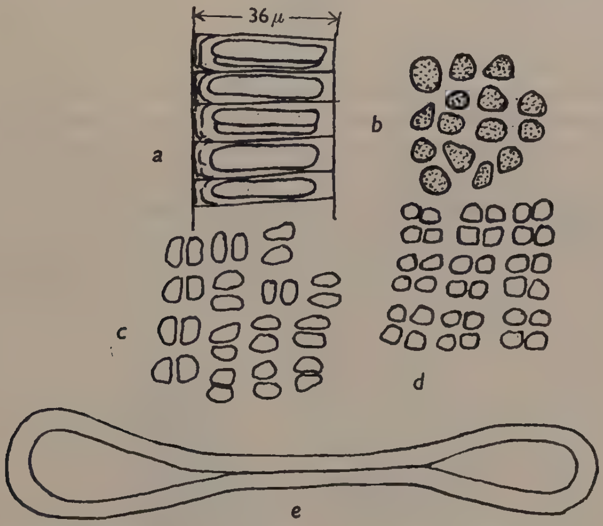

Fig. 43. *Gemina enteromorphoidea*. *a*, membrane; *b–d*, cells in surface view; *e*, T.S. of thallus.

(1) *Gemina enteromorphoidea* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 51, 1952.

Plant simple, compressed, up to 37 cm. long and 5 mm. wide, tubulose, attenuate to the stipe, attached by a minute scutate disk; cells small, 3·75–9·3μ (average 5·5μ) dia., arranged in distinct pairs or fours, the pairs themselves in short rows; single membrane 36μ wide, the outer wall 5μ thick, the inner 4μ, the cells 27μ high in T.S.; colour deep grass green or olive green, adhering moderately to paper. (Fig. 43; Pl. 31.)

DISTRIBUTION. Local: Stewart Is., Campbell Is. Endemic.

This is a very remarkable species, particularly in view of the relationships with allied genera. The arrangement of the cells in pairs or fours is characteristic of the genus *Capsosiphon*, but there is no evidence of any parent mother cell membranes nor are there any areolae. Except for the absence of areolae the species would be very similar to *Capsosiphon aurea* (see p. 429). In fact this species and *Capsosiphon aurea* form a definite series from the normal *Enteromorpha*-type of construction to the normal *C. fulvescens*-type of construction.

The small size of the cells suggests that it is allied to *Enteromorpha bulbosa*, though it differs in the cell arrangement and also in the very elongate cells as seen in T.S. Another interesting feature is seen in the fusion of the central part of the tube to produce an *Ulva*-like arrangement. In this respect it forms, together with *Ulva atroviridis* of South Africa, a transition between the *Enteromorpha*- and *Ulva*-types of construction.

(2) *Gemina ulvoidea* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 52, 1952.

Plant simple, membranaceous, forming a flattened, expanded frond up to 13 cm. long and 7 cm. wide, perforated; cells small, 3·75–9·3μ dia., in pairs or fours, the pairs sometimes arranged in short rows; cells 27μ high in T.S., membrane 70–76μ thick, the outer wall up to 5μ thick.

Distribution. Local: Lyall Bay, Stewart Is. Endemic.

This remarkable form has the same microscopic features as the preceding species but differs from it in habit. Another specimen, which appears referable to this species, has been collected from Lyall Bay.

(3) *Gemina letterstedtioidea* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 52, 1952.

Thallus membranaceous, compressed, up to 8 cm. long and 1 cm. wide, attenuate to a stipe; plants entire or perforate, simple or branched, main thallus or branches linear or expanding into a lobe; cells 7·5–11μ (average 8μ) dia., in pairs, the pairs in short rows, 49μ high in T.S.; membrane 116μ wide, the outer wall up to 7μ thick. (Fig. 44; Pl. 31.)

Distribution. Local: Campbell Is., Auckland Is. Endemic.

This member of the genus has a remarkable superficial resemblance to *Letterstedtia*, but microscopically the paired arrangement of the cells places it in this genus.

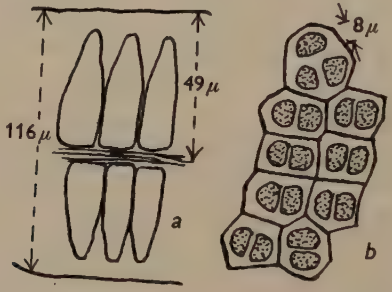

Fig. 44. *Gemina letterstedtioidea*. *a*, membrane; *b*, cells.

(4) *Gemina clavata* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 53, 1952.

Thallus simple, minute, up to 1·5 cm. tall and 0·5 cm. wide, clavate, contorted, attenuate sharply to a narrow stipe; cells small, 3·5–9μ dia., 27μ high, in pairs or fours within the parent cell wall; membrane 70–76μ wide; brownish green in colour. (Fig. 45I; Pl. 31.)

Distribution. Local: Campbell Is. Endemic.

(5) *Gemina linzoidea* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 53, 1952.

Plant up to 27 cm. long and 6 cm. at the widest part, narrowing gradually to a stipe region; upper part of blade laciniate, entire or perforate; cells in pairs, more rarely in threes or fours, surrounded by parent membrane; cells 5–9μ (average 7μ) dia., 41–49μ high in T.S., conical; membrane 116–148μ, outer wall 4–7μ thick; reproductive cells scattered in lower part of thallus, 18–22·5μ dia., olive green; adheres imperfectly to paper. (Fig. 45 II.)

DISTRIBUTION. Local: Stewart Is. General: Cape of Good Hope.

This species probably has a wider distribution. There is agreement in all characters with a specimen from the Cape of Good Hope in Leiden Herbarium. Information about the method of reproduction was obtained from this specimen.

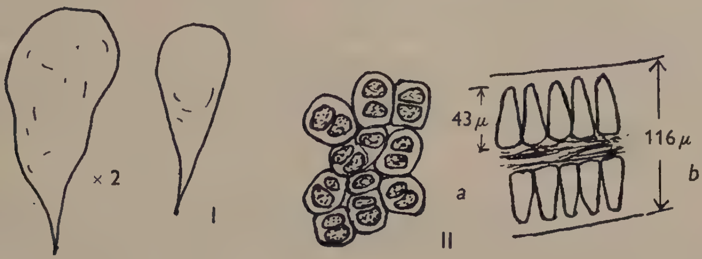

Fig. 45. I. *Gemina clavata*, plants. II. *G. linzoidea*, *a*, cells, *b*, membrane.

Enteromorpha Link

Frond tubular, hollow or solid, slender or ample, simple, proliferous or branched, attached or free-living, the wall consisting of a single layer of cells; all cells, except the very lowest, capable of producing zoospores or gametes.

This is a notoriously difficult genus. The exact limits of the different species are extremely difficult to define. The result has been that the treatment of the genus usually follows one of two methods. On the one hand, it is possible to recognize a large number of species, whilst on the other hand relatively few species are recognized, but they are regarded as occurring in a variety of forms. The present writer prefers the second alternative, and recognizes the following major species, all of which exist in a variety of forms, some being regarded as varieties and others, because of their peculiar habitat, as ecological forms. It seems preferable to give to these forms the names by which they are known in the literature rather than to call them form I, form II, etc., as does Bliding (1939).

Enteromorpha intestinalis. The members of this species are usually unbranched and have a thick membrane (i.e. the wall of the tube), the inner wall being much thickened (see Fig. 47*g*, *h*). The cells are irregularly arranged.

Enteromorpha compressa. The members of this species are usually branched, the branches being constricted at the base. The membrane is thin and the inner wall is not thickened. The cells are irregularly arranged.

Enteromorpha bulbosa. In appearance like certain varieties of both the above two species but differing in the much smaller size of the cells, which also possess thick walls. It may be better to treat this as a distinct variety of *E. intestinalis*.

Enteromorpha nana. The members of this species are characterized by the extremely small size of the cells.

Enteromorpha procera. The plants placed in this species look like *E. compressa* but they are much paler in colour and fade when dried. In the dry state they have a parchment-like appearance. The cells usually show some signs of row arrangement and the walls are commonly thick as compared with those in the *E. compressa* group.

Enteromorpha ramulosa. This is a very common species in New Zealand, and is characterized by the high degree of proliferation, many of the outgrowths being spinous in character. The cells are generally irregularly arranged. This group also includes *E. acanthophora*.

Enteromorpha prolifera. The cells are arranged in rows and the plants are bright grass green in colour.

Enteromorpha clathrata. The cells are arranged in rows and the thallus has branches of successive orders rather than proliferations. The chloroplast is commonly granular.

Enteromorpha crassimembrana. A new species that could perhaps be placed in either the *procera* or *clathrata* group, but the nature of the membrane is so outstanding that it is treated as a separate species.

The elucidation of the innumerable forms of *Enteromorpha* to be found around the shores of New Zealand will not be complete until intensive cultural studies have been undertaken. In at least one case (*E. compressa* var. *australiensis*) there is strong evidence in support of the existence of two generations, one simple and the other branched. A similar phenomenon has already been reported from Europe for *E. prolifera* (Bliding, 1939).

Key to the local species

1.	Cells not arranged in longitudinal rows, except perhaps in the very youngest parts.	**2**
	Cells arranged in longitudinal rows in most of thallus.	**37**
2.	Cells smaller than 8μ dia., usually 3–4μ.	**3**
	Cells larger than 8μ dia.	**8**
3.	Cells in rows at the edge of the thallus.	*E. nana* var. *marginata*
	Cells irregularly arranged throughout.	**4**
4.	Inside wall of membrane thickened.	**5**
	Inside wall of membrane thin.	**7**
5.	Plants tufted, expanding from base, proliferating at apex.	*E. nana* var. *minima* f. *fastigiata*
	Plants elongate.	**6**
6.	Plants broad, bullose.	*E. nana* var. *minima* f. *bullosa*
	Plants filiform, contorted, membrane more than 14μ.	*E. nana* var. *minima*
	Plants filiform, straight, membrane less than 14μ.	*E. nana* var. *minima* ecad *rivularis*
7.	Plants branched at the base, expanding broadly above.	*E. nana* f. *gunniana*
	Plants linear, proliferating throughout.	*E. nana*
8.	Thallus simple.	**9**
	Thallus branched or proliferating.	**19**
9.	Membrane rarely more than 20μ, inner wall not thick, thallus attenuate at both ends.	*E. compressa* var. *biattenuata*
	Membrane more than 20μ thick.	**10**
10.	Plants olive green, cells av. dia. 8μ, walls thick.	**11**
	Plants grass green, cells av. dia. 10–12μ, walls thin.	**12**
11.	Plant linear.	*E. bulbosa*
	Plant short, cornet-shaped.	*E. bulbosa* f. *cornucopiae*
12.	Thallus very pale and thin, inner wall of membrane 35–60μ thick, lamellate.	*E. crassimembrana*
	Thallus otherwise.	**13**
13.	Inner wall of membrane 4μ thick or less.	**14**
	Inner wall of membrane 4–40μ thick, not lamellate.	**15**
14.	Plant small, up to 2·5 cm. in length, dilating to apex.	*E. compressa* var. *australiensis*
	Plant more than 2·5 cm. in length, linear.	*E. compressa* f. *subsimplex*
15.	Thallus attached.	**17**
	Thallus free-living, linear.	**16**
16.	Thallus narrow, not inflated.	*E. intestinalis* f. *tubulosa*
	Thallus wide, inflated.	*E. intestinalis* f. *bullosa*
17.	Thallus small, horn-shaped, often curved.	*E. intestinalis* f. *cornucopiae*
	Thallus linear, or dilating gradually to apex.	**18**
18.	Plants more than 2·5 cm. long.	*E. intestinalis*
	Plants less than 2·5 cm. long.	*E. intestinalis* f. *brevis*

19.	Thallus much branched, axis and branches beset with short simple branches with acute spiny apices.	20
	Thallus branched mainly towards the base, branches more elongate with obtuse apices.	25
20.	Chloroplast granular.	21
	Chloroplast homogeneous.	22
21.	Free-living on mud flats.	*E. clathrata* f. *prostrata*
	Attached.	*E. clathrata* var. *usneoides*
22.	Branchlets attenuate at the base, cells in indistinct rows.	*E. ramulosa* var. *acanthophora*
	Branchlets broad at base, cells irregularly arranged.	23
23.	Thallus confervaceous, no main axis.	*E. ramulosa* f. *minor*
	Main axis distinct.	24
24.	Membrane 20–28μ.	*E. ramulosa* f. *spinescens*
	Membrane 30–45μ.	*E. ramulosa* f. *robusta*
25.	Average diameter of cells 8μ or less, plants olive green	26
	Average diameter of cells exceeding 8μ, plants grass green or pale green.	27
26.	Plants small, brownish, branched at the base.	*E. bulbosa* f. *cornucopiae*
	Plants large, branches with foliar proliferations.	*E. bulbosa* f. *foliacea*
27.	Plants pale or yellow green, parchment-like when dry, intercellular walls thick.	20
	Plants grass green, paper-like when dry, intercellular walls thin.	36
28.	Thallus branched only at the base.	29
	Thallus branched throughout.	32
29.	Plants less than 2 cm. long, branches scarcely dilating.	30
	Plants more than 2 cm. long, branches dilating.	31
30.	Membrane 25–28μ, branchlets polysiphonous.	*E. procera* f. *minuta*
	Membrane 20–24μ, apices of branchlets monosiphonous.	*E. procera* f. *novae-zelandiae*
31.	Plant very pale, branches cuneate, cell walls very thick.	*E. procera* f. *chlorotica*
	Plant pale green, branches linear, dilating gradually.	*E. procera* f. *eramosa*
32.	Main axis broad with numerous long linear proliferations.	*E. procera* f. *prolifica*
	Main axis fine with short proliferations or branches.	33
33.	Plant delicate, adhering well to paper.	*E. procera* f. *denudata*
	Plant coarser, not adhering to paper.	34
34.	Branches mainly opposite, membrane 21–30μ.	*E. procera* f. *opposita*
	Branches irregular, membrane 15–24μ.	*E. procera* f. *subundulata*
35.	Cells in rows in younger branches.	36
	Cells irregularly arranged throughout.	*E. compressa*
36.	Plant 2 cm. or less in length.	*E. compressa* f. *australiensis*
	Plant more than 2 cm. in length.	*E. compressa* f. *lingulata*
37.	Thallus simple.	38
	Thallus branched or with proliferations.	42
38.	Thallus solid or almost solid, pale green.	39
	Thallus a definite tube.	41
39.	Thallus of two rows of cells.	*E. percursa*
	Thallus of more than two rows of cells.	40
40.	Chloroplast homogeneous, filling the cell.	*E. prolifera* var. *torta*
	Chloroplast granular, not filling the cell.	*E. clathrata* var. *ralfsii*
41.	Thallus attached, dilating to apex.	*E. prolifera* var. *flexuosa*
	Thallus free-living, linear.	*E. prolifera* f. *pilifera*
42.	Thallus with branches of successive orders, chloroplast granular.	43
	Thallus with proliferations, chloroplast homogeneous.	45
43.	Thallus branched at base only.	*E. clathrata* f. *pumila*
	Thallus branched throughout, confervaceous.	44
44.	Branches ending in a long monosiphonous portion, membrane 24–28μ thick.	*E. clathrata* var. *plumosa*
	Branches ending in a short monosiphonous portion, membrane 18–24μ thick.	*E. clathrata* var. *angustimembrana*
45.	Branches ending in a single series of cells.	*E. prolifera* f. *crinita*
	Branches not ending in a single series of cells.	*E. prolifera*

(1) *Enteromorpha intestinalis* (L.) Grev.

Greville, *Alg. Brit.* p. 179, 1830; Collins, Green. Alg. N. Amer. p. 204, 1909; Harv. in Hooker, *Fl. Nov. Zel.* **2**, 264, 1855; *Handb. N.Z. Flora*, p. 716, 1867.

Thallus up to 1 m. long and 1 cm. broad, membranous, attenuate at the base, elongate, tubulose and stipitate; frond simple, very occasionally branched at the base, clavate, compressed or inflated; attachment organ a minute scutate disk; cells arranged irregularly, 8–20μ, average 15μ dia., 12–30μ high in T.S., 8–16μ wide; cells in stipe 16–30μ high in T.S., 7–14μ wide; chloroplast filling the cell; membrane 20–65μ wide, the inner wall strongly thickened, 4–30μ; colour from full herbaceous green to pale, semi-transparent yellow green. (Fig. 47, *h*.)

DISTRIBUTION. Local: throughout New Zealand. General: cosmopolitan.

Although the species is widely distributed, it does not appear to be common. Specimens in herbaria show that in the past it has been confused with *E. compressa* var. *biattenuata* and *E. compressa* f. *subsimplex*. It differs from both these in possessing a thickened inner wall to the membrane.

(2) *Enteromorpha intestinalis* f. *brevis* Schiffn. (mscr.)

Plants with the characters of the above but differing from it in the small size, the thallus always being less than 2·5 cm. in length.

DISTRIBUTION. Local: Waitangi, Narrow Neck, Moeraki (lime encrusted), Whangaparaoa Hds., Eastbourne and probably elsewhere. General: Europe and probably elsewhere.

This form is usually found towards H.W.M. on exposed, rocky seashores. It is very similar to f. *cornucopiae* but the two forms differ in their ecological requirements.

(3) *Enteromorpha intestinalis* f. *bullosa* Hauck

Hauck, Meeresalg. Deutschl. p. 427, 1885.

Thallus simple, bullose, inflated or subcompressed, substance somewhat attenuated: cells irregularly arranged, average dia., 12–15μ; membrane 20–28μ, inner wall thickened: free-living, floating in brackish or fresh water. Adheres well to paper.

DISTRIBUTION. Local: Napier (as *E. intestinalis* f. *cylindracea*), Green Is. lagoon, Porirua. General: Europe, Canary Is., Bermuda, Vancouver, New England (U.S.A.).

The plant from Napier was collected by von Müller and is in herb. Univ. Lund.

(4) *Enteromorpha intestinalis* f. *cornucopiae* Lyngb.

Newton, *Handb. Brit. Seaw.* p. 70, 1931; Harv., *Phyc. Brit.* pl. 304, 1849–51.

Thallus abbreviated, simple, arising from a narrow stipe, 1–6 cm. long, 1–15 mm. broad, club or cornet-shaped, cylindrical or compressed, often wrinkled; cells irregularly arranged, cells of lower part of thallus 6–10μ dia., in upper part 8–24μ (average 8–15μ) dia.; cells above stipe 16–24μ high in T.S., 6–10μ broad; membrane 40μ thick (average), the inner wall 4–30μ thick; colour usually a dark, intense green, rarely pale green; adheres fairly well to paper. (Fig. 46.)

DISTRIBUTION. Local: Bluff (90 Mile Beach), Waitata Rocks (Russell), Rangitoto, Paturau North, Island Bay. General: Europe, Iceland, Greenland, Algeria, Cape Town, Massachusetts, Adriatic, Alexandria.

This form is always associated with an influx of fresh water.

(5) *Enteromorpha intestinalis* f. *tubulosa* Kütz.

Kütz., *Tab. Phyc.* **6**, tab. 32, II, 1856 as *E. tubulosa*.

Thallus slender, elongate, crisped or contorted, simple or with hair-like branchlets, tubular or subcompressed; cells in main thallus arranged irregularly, 8–12μ dia. at base or apex, 8–32 × 8–24μ in rest of thallus, 8–20μ high in T.S., 8–15μ wide; cells in smaller branches often in rows; membrane 10–36μ, the inner wall 4–20μ thick; chloroplasts usually filling the cell; colour grass-green to whitish green; plants commonly free-living, much entangled. (Fig. 47.)

Distribution. Local: Parnell, Napier, Lyall Bay, Ahuriri lagoon, Portobello, Stewart Is., Chatham Is., Porirua, Eastbourne. General: Europe, Finland, Canaries, Iceland,

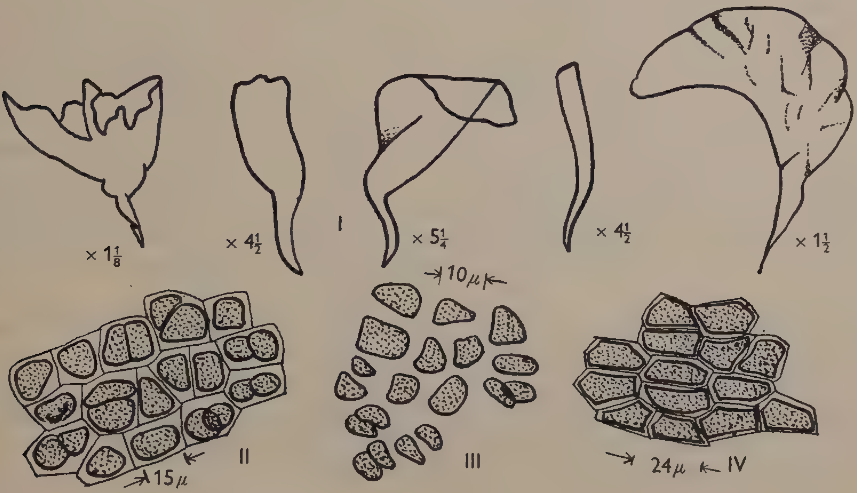

Fig. 46. *Enteromorpha intestinalis*, f. *cornucopiae*. I, plants; II, cells of stipe; III, cells of apical region; IV, cells of centre.

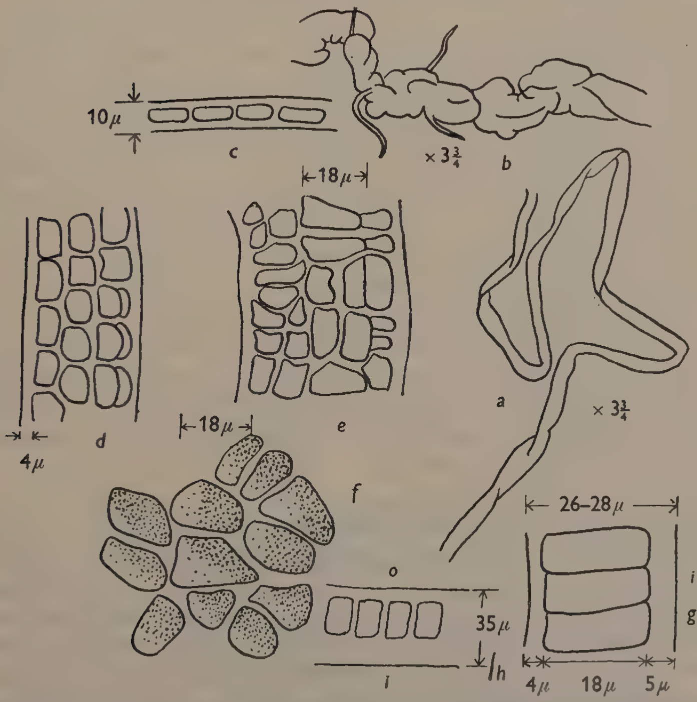

Fig. 47. *a–g*, *Enteromorpha intestinalis* f. *tubulosa*: *a*, *b*, plants; *c*, *g*, membrane of young and old plants; *d*, *e*, portions of young threads; *f*, cells. *h*, *Enteromorpha intestinalis*: membrane. *i* = inner wall, *o* = outer wall of membrane.

Greenland, St Lawrence to Virginia, Vancouver to lower California, Guadeloupe, Rio de Janeiro, Philippines, Mauritius, Formosa, Japan, Port Said, St Helena, Cape Town.

In appearance this form is very similar to *E. prolifera* f. *pilifera*, but it differs microscopically because the cells are irregularly arranged and the inner wall of the membrane is thickened.

(6) *Enteromorpha compressa* (L.) Grev.

Greville, *Flor. Brit.* p. 180, pl. 18, 1830; Collins, Green. Alg. N. Amer. p. 207, 1909; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877 (*pro parte*); Harv. in Hooker, *Fl. Nov. Zel.* **2**, 264, 1855; *Handb. N.Z. Flora*, p. 716, 1867; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926.

Frond up to 3 dm. long and 20 mm. wide, attached by a small disk, membranaceous, branched richly or poorly throughout whole of thallus, branches narrow at first, gradually dilating to an obtuse apex; thallus tubular or collapsing, more or less compressed, sometimes constricted at intervals; cells irregularly arranged, 4–20μ (average 10–15μ) dia., 20–30μ high in T.S., 8–12μ wide; cells sometimes more or less in rows in young parts; chloroplast filling the cell; membrane not markedly thickened on inside; colour dull to bright green.

Distribution. Local: Mairangi Bay, Petone, Wellington, Nelson, Banks Peninsula, St Clair, Invercargill, Stewart Is., Port Elizabeth. General: cosmopolitan.

This species is not so common as has been formerly supposed. This is because it has been confused with forms of *E. procera*. It differs from these in the brighter green colour, the thin membrane and thin-walled cells. The plant from Invercargill was collected by von Müller and is in the herbarium at Lund University.

(7) *Enteromorpha compressa* var. *australiensis* (Chapm.) comb. nov.

Chapman, *J. Bot. Lond.* p. 265, 1940 (as *E. prolifera* var. *australiensis*).

Thallus small, up to 2·5 cm. long, tubular, caespitose; existing in two forms (probably alternate generations); one form simple, unbranched, dilating to the apex, membrane 20–28μ thick, inner wall 4–8μ thick; the other form much branched, especially towards the base; branches obtuse at apex with numerous proliferations, not attenuate at the base and with acute apices; membrane 16μ thick, inner wall not thickened; cells in indistinct rows in the younger parts, irregularly arranged elsewhere; cells 8–20μ (average 12–14μ) dia., 16–19μ high in T.S., chloroplast homogeneous, not always filling the cell in the branched form. (Fig. 48.) V.W.L. 129 as *E. compressa* f. *obtusa*.

Distribution. Local: Bay of Islands, Stanmore, Narrow Neck, Wellington, Taylor's Mistake, St Clair, Kermadec Is. (?). Endemic.

This species appears to be restricted to positions near h.w.m. When grown in culture the two forms develop at different seasons of the year and the one appears to give rise to the other. Final cultural proof is not yet available but the presumptive evidence is very strong. It is believed that the two forms represent the two generations, one sexual, the other asexual. The plant has been removed from the *prolifera* to the *compressa* group in the light of the new information available.

(8) *Enteromorpha compressa* var. **biattenuata** var.nov.

Thallo ad 71 cm. alto et 1·5 cm. lato, membranaceoso, attenuato ad stipitem et apicem, simplice aut parce ramosis, ramis attenuatis ad parte inferioribus et superioribus, compresso aut inflato; per discum minutum scutatum adfixo; cellulis irregulariter dispositis, 4·2–7·5μ dia. in stipo, 7·5–22·4μ (plerumque 15μ) in fronde, 15–16μ altis, lamellis intercellulis tenuis; chloroplaston per tota cellula; membrana 18–20μ crassa, pariete interiore ad 3·5μ.

Thallus up to 71 cm. long and 1·5 cm. wide, membranous, attenuate at base and apex, tubulose, simple or sparsely branched with long slender branches attenuate at base and apex, compressed or inflated; attachment organ a minute scutate disk; cells arranged irregularly, 4·2–7·5μ dia. in stipe 7·5–22·4μ (average 15μ) in expanded portion, 15–16μ tall, intercellular walls thin except in stipe; chloroplast filling the cells; membrane 18–20μ thick, the inner wall up to 3·5μ thick; colour pale grass green; adheres moderately to paper. (Fig. 49, Pl. 32.) Type specimen in herb. V. W. Lindauer, from Bay of Islands (Deepwater cove).

DISTRIBUTION. Local: Bay of Islands, Wellington, Lake Ellesmere, St Clair, Portobello. Endemic.

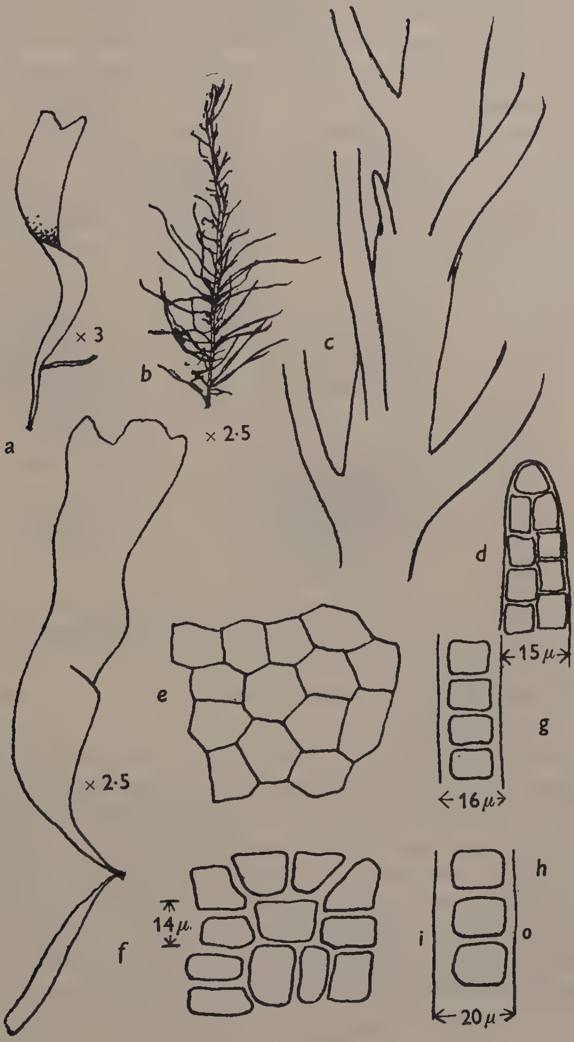

Fig. 48. *Enteromorpha compressa* var. *australiensis*: *a*, plants of simple form; *b*, plant of branched form; *c*, ditto, enlarged; *d*, apex of branch; *e*, cells of simple form; *f*, cells of branched form; *g*, membrane of branched form; *h*, membrane of simple form. *i* = inner wall, *o* = outer wall of membrane.

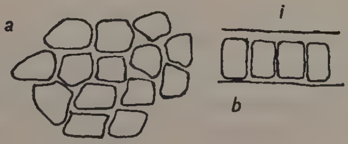

Fig. 49. *Enteromorpha compressa* var. *biattenuata*: *a*, cells; *b*, membrane.

It is possible that this variety exists in two forms, one longer and broader and the other narrower and with a greater tendency to branch. The simple form has been mistaken in the past for *E. intestinalis* but it does not possess the thickened inner wall to the membrane.

(9) *Enteromorpha compressa* var. *lingulata* (J. Ag.) comb. nov.

J. Ag., *Till. Alg. Syst.* **6**, p. 143, 1882; Börg., Mar. Alg. D.W. Ind. p. 7, 1913; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926 (all as *E. lingulata* J. Ag.).

Thallus large, up to 30 cm. long, 3–6 mm. wide, branched from base to apex, rather more so at base; branches linear, dilating somewhat towards apices; subcompressed or compressed, usually constricted at the base; cells often arranged in irregular rows in secondary branches, arranged irregularly in main axis; cells 4–16μ long × 8–12μ wide; membrane 15–30μ thick; the inner wall up to 6μ thick, light to dark grass green. (Fig. 50.)

DISTRIBUTION. Local: Russell, Wellington, Akaroa, Kaha Pt, Greymouth, Wycliffe, St Clair, Warrington, Brighton. General: Atlantic Shores of Europe and North America, Baltic, Spitzbergen, Mediterranean, Gulf of Mexico, Tasmania, Australia, West Indies.

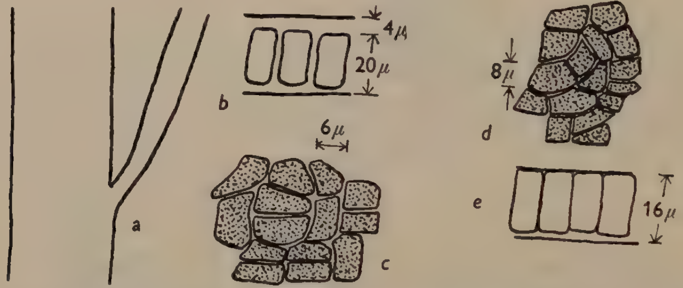

Fig. 50. *a–c*, *Enteromorpha compressa* var. *lingulata*: *a*, base of branch; *b*, membrane; *c*, cells. *d*, *e*, *E. compressa* f. *subsimplex*: *d*, cells; *e*, membrane.

(10) *Enteromorpha compressa* f. *subsimplex* Le Jol.

J. Ag., *Till Alg. Syst.* **6**, p. 137, 1882.

Frond tenuous above the stipe, up to 18 cm. long and 5 mm. wide, dilated or compressed, simple, linear, or slightly expanded towards the apex, arising from a minute scutate disk; margin of thallus even, sometimes constricted at intervals; cells irregularly arranged, 8–15μ dia., 8–20μ high in T.S. and 10–15μ wide; membrane 16–25μ thick; walls unthickened; colour grass green, adhering well to paper. (Fig. 50.)

DISTRIBUTION. Local: Piha, Muriwai, Arkles Bay, Te Haruhi Bay, Stanmore, Rangitoto, Horoera, Greymouth, Island Bay, St Clair. General: Europe, New England (U.S.A.), Gulf of Mexico, Brazil, Oregon.

This form can be mistaken for others unless careful attention is given to the cell arrangement and thickness of the membrane and its walls.

(11) *Enteromorpha prolifera* (Muell.) J. Ag.

J. Ag., *Till Alg. Syst.* **6**, p. 129, pl. 4, pp. 103–4, 1882; Kütz., *Tab. Phyc.* **6**, tab. 42, fig. 2, 1856.

Plant up to 50 cm. long and 2 mm. wide, membranous, attenuate from a holdfast and in the simple form also at the apex; thallus simple (one generation) or with few to many proliferations varying in length, themselves with numerous secondary proliferations (other generation); thallus slender, tubular or collapsing, often loosely intricate, larger plants of the simple generation sometimes being inflated or crinkled; cells in rows in branches, less distinctly so in the older parts, 4–16μ wide × 5–24μ long, 10–24μ high in

T.S., 8–17μ wide; chloroplast filling the cell; membrane 15–44μ wide, often with both walls up to 8μ thick; attached or free-living; dull green in colour; branched generation tends to disintegrate when dry. (Fig. 51.)

DISTRIBUTION. Local: Maketu, George Sound, Chatham Is., Waikouaiti, Porirua, Otago Harbour, Puketeraki, Brighton, Portobello, St Clair, Allen's Beach. General: probably cosmopolitan in colder waters.

Bliding (1939) has demonstrated that this species exists in a much-branched summer phase and a simple phase. In the past the latter has probably been described as *E. flexuosa* (see below) or as *E. compressa* f. *subsimplex*.

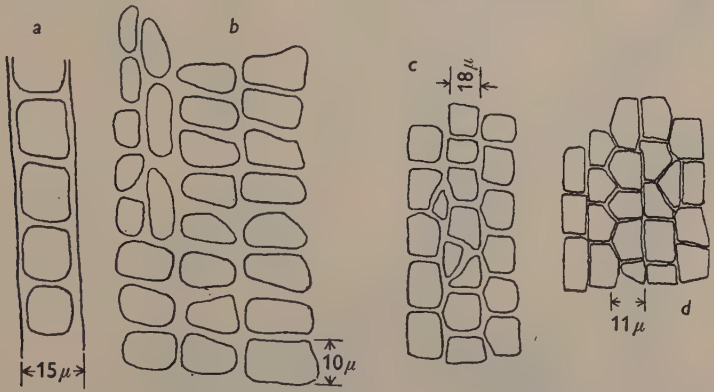

Fig. 51. *a*, *b*, *Enteromorpha prolifera*: *a*, membrane; *b*, cells. *c*. *Enteromorpha prolifera* f. *pilifera*: cells. *d*. *Enteromorpha prolifera* var. *flexuosa*: cells.

(12) *Enteromorpha prolifera* var. *flexuosa* Wulf.

J. Ag., *Till. Alg. Syst.* **6**, p. 127, 1882; Collins, Green Alg. N. Amer. p. 203, 1909; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926 as *E. flexuosa*.

Thallus simple, rarely branched, up to 22 cm. long and 5 mm. wide, dilating gradually from a narrow stipe, flexuous, tubular or compressed, constricted slightly at intervals, membranaceous, obtuse at the apex; cells in rows, 8–16μ long × 6–12 (–25)μ wide; walls thick, chloroplast filling the cell; membrane 16–22μ wide, not thickened on inside, outer wall up to 4μ thick; light grass or grey green. (Fig. 51.)

DISTRIBUTION. Local: Russell, Coromandel, Te Kaha, Lyall Bay, Lake Ellesmere, Queen Charlotte Sd., Sumner, Waimakerere, Blackhead, St Clair. General: cosmopolitan in warmer waters.

There is no doubt that further work is required on the status of this form, which may eventually turn out to be the alternate generation of a branched species (see *E. compressa* var. *australiensis*). It is in fact somewhat surprising to find it occurring in the relatively cool waters of New Zealand, especially those of Queen Charlotte Sound and Portobello.

(13) *Enteromorpha prolifera* var. *crinita* Roth

Collins, Green Alg. N. Amer. p. 199, 1909; Hylmö, Stud. Grünalg. p. 18, pl. 1, figs. 18–20, pl. 2, fig. 45, 1916 as *E. crinita*.

Frond filiform, setaceous, 10–60 cm. long and up to 4 mm. wide, much and repeatedly branched, branches attenuate at the apex, tubular, terminating in a monosiphonous portion, some branchlets wholly monosiphonous; cells subquadrate, rotund, arranged in rows, row arrangement partially obscured in old parts of the thallus; cells of branches 10–15μ dia., of main thallus 5–30μ (average 20μ) dia., walls sometimes thickened; membrane 23–29μ, the outer wall slightly thickened; plants light or dull green, adheres moderately to paper. (Fig. 52.)

Distribution. Local: Russell (young?), Portobello, Doubtful Sd, Stewart Is. General: Atlantic coast of Europe, Baltic, Mediterranean, Red Sea, Nova Scotia to central Mexico, Aleutians to S. California, Sulu Is., Thursday Is., Samoa, Philippines, S. Australia.

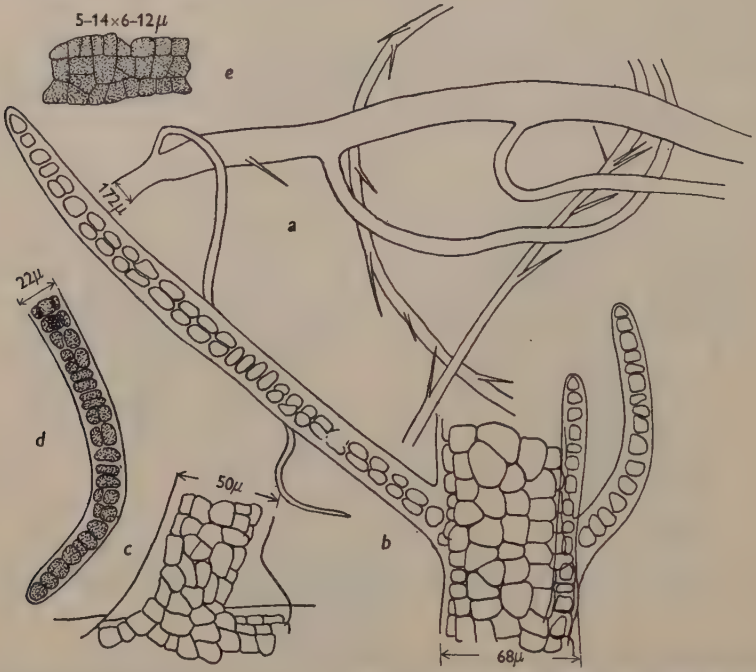

Fig. 52. *Enteromorpha prolifera* var. *crinita*: *a*, portion of plant; *b*, same enlarged; *c*, base of large branch; *d*, monosiphonous apex; *e*, cells.

(14) *Enteromorpha prolifera* f. *pilifera* Kütz.

Kütz., *Tab. Phyc.* **6**, tab. 30, fig. 3, 1856; Collins, Green Alg. N. Amer. p. 203, 1909 (as *E. prolifera* var. *tubulosa*).

Threads up to 2 dm. long, tubular or subcompressed, plain or contorted, tangled, filiform, 36μ–5 mm. wide, average 500μ, more or less regular in dia. throughout its length, usually simple, sometimes with short mono- or polysiphonous proliferations; cells in rows 8–24 (–40)μ long × 28μ wide, 10–14μ high in T.S., chloroplast filling the lumen; membrane 13–24μ thick, walls usually not much thickened; free living; light or pale green in colour; slimy to touch when fresh. (Fig. 51.) V.W.M. 81.

Distribution. Local: Russell, Deepwater Cove, Helensville, Motutapu, Poverty Bay, Lyall Bay, Otipua Lagoon, Waikanae Estuary, Kaikorai, St Clair, Pegasus (Stewart Is.). General: almost cosmopolitan.

This form is readily recognized by the long, linear, tubular, usually unbranched, threads, with cells arranged in regular rows. It is commonly found lying free-living on salt marshes or mangrove swamps.

(15) *Enteromorpha prolifera* var. *torta* (Mert.) comb.nov.

Newton, *Handb. Brit. Seaw.* p. 68, 1931 (as *E. torta*); Laing, *Trans. N.Z. Inst.* **57**, 135, 1926 (as *E. percursa*).

Frond filamentous, 30–80μ wide, forming entangled strata; threads simple or with occasional branches, tubular or almost solid; main thallus consisting of a small number

(2–8) of cell rows; cells 8–16μ wide × 5–20μ long; walls thin, chloroplast homogeneous, filling the cell. Colour bright grass green; growing unattached. (Fig. 53.)

Distribution. Local: Orongo Bay, Frenchman's Bay, Waitangi, Creeks on Waiuku Rd, St Clair, Porirua. General: Europe, Baltic, Gulf of Mexico, Lower California to Mexico, Indonesia.

This is described in most works as *Enteromorpha torta*, but the present writer believes that it represents the final reduced form of *E. prolifera* f. *pilifera*.

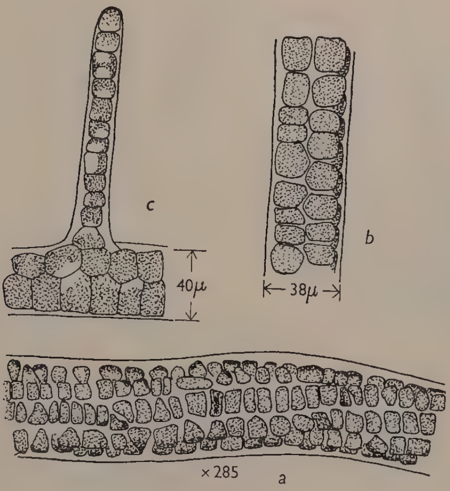

Fig. 53. *Enteromorpha prolifera* var. *torta*: *a*, portion of large plant; *b*, portion of small plant; *c*, proliferation.

(16) *Enteromorpha bulbosa* (Suhr) J. Ag. f. *novae-hollandiae* (Kütz.) comb.nov.

Kütz., *Tab. Phyc.* **6**, tab. 38, fig. B, 1856 (as *E. compressa* f. *novae-hollandiae*); J. Ag., *Till Alg. Syst.* **6**, p. 139, 1882, as *E. bulbosa* f. *australica*; Laing, *Trans. N.Z. Inst.* **57**, 134, 1926.

Thallus up to 12·5 cm. long and 6 mm. wide, simple or branched, mainly at the base, narrow above the stipe, gradually dilating, tubular or collapsing; branches narrow at base, dilating upwards, occasionally beset with small spine-like proliferations; cells small, irregularly arranged, walls thick, 3–4μ; cells 4–12μ (average 6–8μ) dia., 17–24μ high in T.S.; chloroplast homogeneous in young part of thallus, sometimes granular in older part; membrane 20–36μ thick, inner wall 4–8μ, the outer 3–4μ thick; olive green in colour; adheres imperfectly to paper. (Fig. 54.) V.W.L. 55.

Distribution. Local: widely distributed throughout the Dominion, Kermadecs, Chatham Is., Campbell Is. General: Australia, Tasmania.

This species is very common in New Zealand, and has been mistaken for both *E. intestinalis* and *E. compressa*. It differs from both of these by the small size of the cells. There is a specimen collected by Berggren in herb. Univ. Lund labelled *E. compressa*, and one in Kützing's herbarium at Leiden (H.L. Bat. 938,19/138) labelled *E. compressa* f. *complanata*.

(17) *Enteromorpha bulbosa* f. *foliacea* Chapm.

Chapman, *Farlowia*, **3** (4), 496, fig. 3, 1949.

Plants similar in size to the previous form, usually branched near the base, the branches beset with small flattened proliferations attenuate at base and apex, apex obtuse; cells small, irregularly arranged, 15–16μ, average 8–10μ dia., 15μ high; membrane 22μ thick, walls 5μ thick on inside. (Fig. 55.)

Distribution. Local: Manakau (Puketutu Is.), Wanganui River, Seatoun, Evans Bay, Green Is. lagoon, St Clair. General: S. Australia, probably elsewhere.

The plants from Green Is. lagoon were very large and luxurious. This may be a result of the habitat conditions.

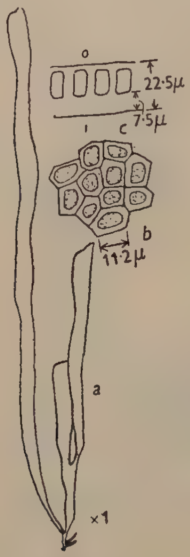

Fig. 54.

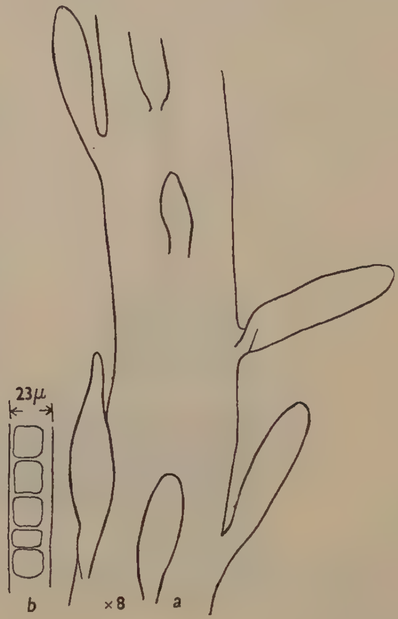

Fig. 55.

Fig. 54. *Enteromorpha bulbosa* f. *novae-hollandiae*: *a*, plant; *b*, cells; *c*, membrane.

Fig. 55. *Enteromorpha bulbosa* f. *foliacea*: *a*, part of plant; *b*, membrane.

(18) *Enteromorpha bulbosa* f. **cornucopiae** form.nov.

Planta ad 2 cm. alta, apicis latis, attenuata ad stipitem.

Plants up to about 2 cm. long, apex broad, attenuate to a narrow stipe, tubular or compressed; cells small, irregularly arranged, similar in size to those of *novae-hollandiae*, membrane also similar. (Fig. 56.) Type specimen P.R.B. 22,775 from Moa Pt.

Distribution. Local: Gannet rocks, Moa Point, Greymouth, Chatham Is., Auckland Is. Endemic.

This form may represent a seasonal condition but the information at present available is not sufficient to justify this assumption.

(19) *Enteromorpha nana* (Sommerf.) Bliding

Newton, *Handb. Brit. Seaw.* p. 71, 1931 (as *E. minima*); Bliding, *Bot. Not.* p. 84, figs. 1–6, 1939; Laing, *Trans. N.Z. Inst.* 57, 135, 1926 (as *E. minima*).

Thallus tangled, gregarious, small, 5–20 cm. long, usually not more than 5 cm., $\frac{1}{3}$–2 mm. wide, simple or proliferating, tubular or collapsing, frond dilating above the stipe, cuneate-linear, obtuse; cells rounded or polygonal, irregularly arranged, except in smaller proliferations or young parts of thallus, 3–8μ dia., 6–9μ high, 5–6μ wide in T.S.; chloroplast filling the cell; membrane 8–16μ, inner wall not thickened; colour dark or golden green; free-floating or epiphytic. (Fig. 57.)

Distribution. Local: Russell, Warkworth (Mick's Creek), Piha, Little Barrier Is., Narrow Neck, Manakau (mangrove swamp on leaves), Wellington, Lyttelton, St Clair, Otago Harbour, Black Head, Dunedin Wharf, Stewart Is., Porirua, Island Bay.

General: more or less cosmopolitan in colder waters.

This species is frequently described in the literature as *E. minima*, but Bliding (ibid.) has shown that its correct name must be *E. nana*. At certain seasons it is found covering the lower leaves of the mangrove.

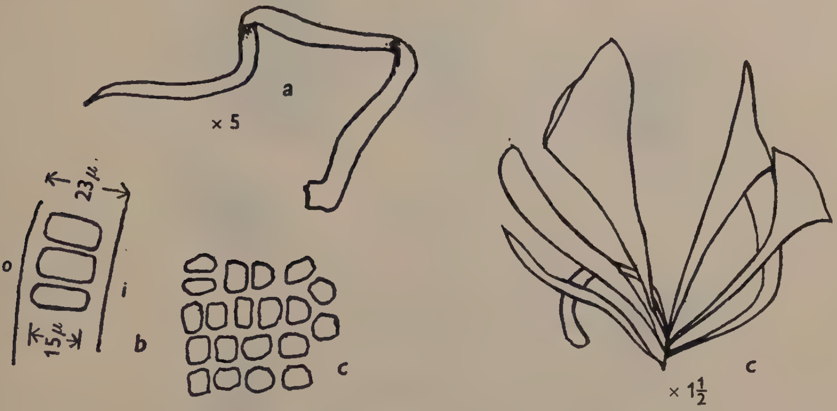

Fig. 56. *Enteromorpha bulbosa* f. *cornucopiae*: *a*, *c*, plants; *b*, membrane; *c*, cells.

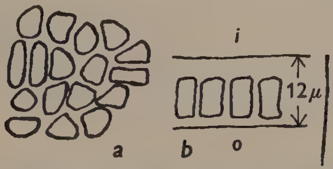

Fig. 57. *Enteromorpha nana*: *a*, cells; *b*, membrane.
i=inner wall, *o*=outer wall.

(20) *Enteromorpha nana* f. *gunniana* (J. Ag.) comb.nov.

J. Ag., *Till Alg. Syst.* **6**, p. 122, 1882 (as *E. gunniana*).

Plant small, attached, dilating upwards from a narrow stipe, becoming linear or clavate; cells small, irregularly arranged, 4μ average dia., membrane 16–20μ, both walls slightly thickened. (Fig. 58.)

Distribution. Local: Russell, Robinson's Bay, Island Bay and probably elsewhere. General: Australia, Tasmania.

This form is intermediate between *E. nana* and *E. nana* var. *minima* in the nature of the principal character, the membrane. It is wider than *E. nana* and the walls are not so thick as in var. *minima*. According to Agardh (loc. cit.), who described *E. gunniana*, it differs also in having a row arrangement of the cells. Such a row arrangement is not visible in specimens in Agardh's own herbarium nor in the specimens from New Zealand. It has clearly only varietal status at the most.

(21) *Enteromorpha nana* var. *minima* (Bliding) comb.nov.

Collins, Green Alg. N. Amer. p. 204, 1909 (as *E. micrococca*); Hylmö, Stud. Grünalg. p. 5, pl. 1, fig. 3, pl. 2, fig. 7, 1916 (as *E. micrococca*).

Plants gregarious, 4–12 cm. long, 5–6 mm. wide, tubular or compressed, simple, dilating from a stipe when present, sometimes slightly branched, curled, twisted and contorted, often proliferating from open apices; cells small, polygonal, irregularly arranged (there may be some indication of row arrangement in the youngest parts), 2–6μ (average 4μ) dia., 6–9μ high in T.S., chloroplast filling the cell; membrane 10–38μ wide, usually 16–25μ, inner wall much thickened, especially in older parts: colour grass green but lighter than *E. nana*, free-floating or attached. (Fig. 59.)

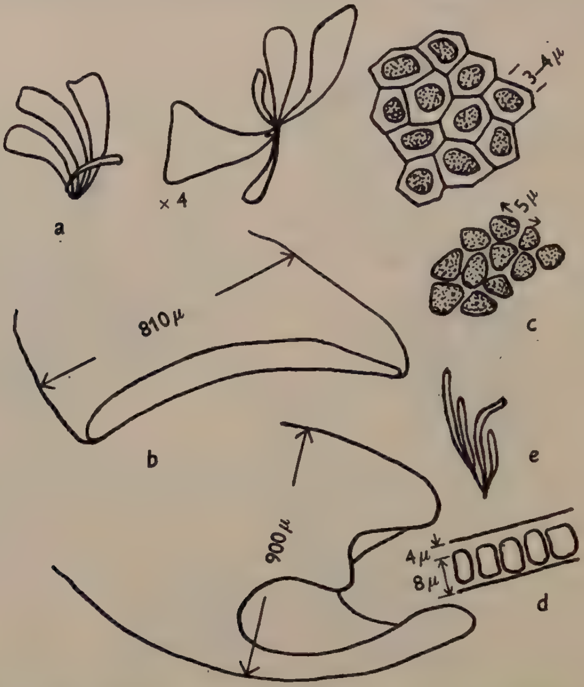

Fig. 58. *Enteromorpha nana* f. *gunniana*: *a*, plants from New Zealand; *b*, apices; *c*, cells; *d*, membrane; *e*, plant from type sheet in herb. Ag. (XI), collected in George Town, Tasmania.

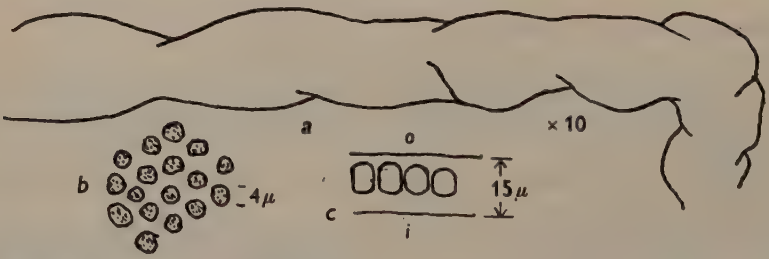

Fig. 59. *Enteromorpha nana* var. *minima*: *a*, portion of thallus; *b*, cells; *c*, membrane. *i* = inner wall, *o* = outer wall.

DISTRIBUTION. Local: Orewa, Queen Charlotte Sound, Lyttelton, Timaru, Waikanae salt marsh, Portobello, Allen's Beach, Stewart Island. General: more or less cosmopolitan in all colder waters.

Bliding (1938) described this form as *E. minima*, but the present writer does not consider that it is of specific status as intermediates (e.g. *E. nana* f. *gunniana*) are known. It is found in colder waters than *E. nana*, and in New Zealand is so far confined to the South Island. This form is described in many works as *E. micrococca* or as *E. micrococca* var. *tortuosa*.

(22) *Enteromorpha nana* var. *minima* ecad *rivularis* (Collins) comb.nov.

Collins, Green Alg. N. Amer. p. 102, 1909 (as *E. minima* var. *rivularis*).

Thallus up to 50 cm. long, 5 mm. wide, tubular, delicate, much branched, branches tapering to the apex and rebranched; cells irregularly arranged, rounded or polygonal, 3–8μ dia., average 5–6μ, 4·5–5μ high in T.S., walls thickened in older parts of thallus, chloroplast filling the cell; membrane 12–14μ, inner walls 3·5–6μ, outer 1·5–2μ; adheres well to paper. Marine and fresh water. (Fig. 60; Pl. 33.)

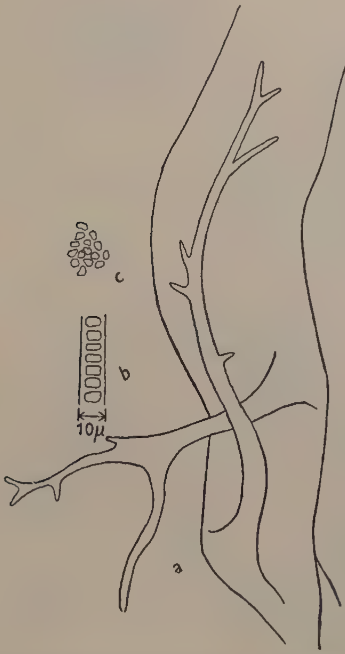

Fig. 60. *Enteromorpha nana* var. *minima* ecad *rivularis*: *a*, part of thallus; *b*, membrane; *c*, cells.

Distribution. Local: Piha stream*, Lake Karapiro*, South Karori Stream*, Sinclair Head, Castle Pt., Pegasus, Cunning Cove. General: Unalaska, California.

The New Zealand plants agree with material from California. It is suspected that it is an ecological form, hence the use of the term ecad.

One very peculiar plant from Sinclair Head (Pl. 33) and another from the South Karori stream appear to belong here. In the former, numerous elongate threads arise from a broad, flattened expansion. The presence of the flattened expansion does not seem to justify the creation of a new form. There is also a broad, flattened expansion in the other specimen (from Karori) which is attenuate to a basal region.

(23) *Enteromorpha nana* var. *minima* ecad *fastigiata* (Chapm.) comb.nov.

Chapman, *Farlowia*, **3** (4), 495, fig. 2, 1949.

Plants minute, up to 5 mm. high, tufted, branches expanding up to 200μ wide from an attenuated base; apex of each branch profusely beset with numerous proliferations, proliferations rare elsewhere; cells arranged irregularly, 4–6μ dia., 5–8μ high, walls thick, chloroplast filling the cells; membrane 25–28μ thick, wall about 12μ thick on the inside and about 8μ on the outside. (Fig. 61.)

Distribution. Local: Stanmore Bay. Endemic.

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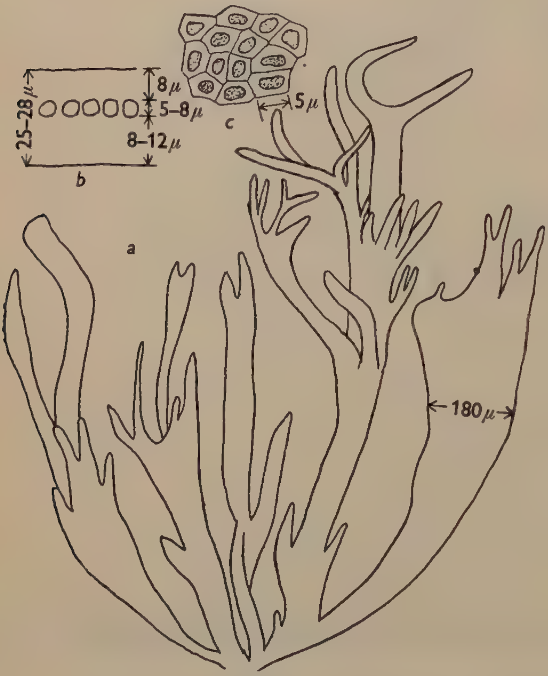
* Fresh water.

(24) *Enteromorpha nana* var. *minima* ecad *bullosa* (Gardn.) comb.nov.

Setchell & Gardner, Mar. Alg. Pacif. N. Amer., Chlorophyceae, p. 249, 1920 (as *E. micrococca* f. *bullosa*).

Frond large, up to 5 cm. long and 1 cm. wide, simple, inflated, bullose, with numerous short projections; cells small, irregularly arranged, 3–8μ (average 4–5μ) dia., 6–12μ high in T.S., membrane 18–24μ wide, the inner wall 7–10μ thick; plants light green; does not adhere to paper. (Fig. 62.)



Fiig. 61.

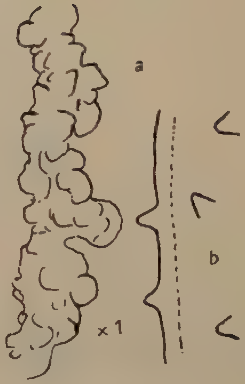


Fig. 62.

Fig. 61. *Enteromorpha nana* var. *minima* ecad *fastigiata*: *a*, plant; *b*, membrane; *c*, cells. (After Chapman.)

Fig. 62. *Enteromorpha nana* var. *minima* ecad *bullosa*: *a*, part of thallus; *b*, same enlarged.

Distribution. Local: Waikanae Salt Marsh, and probably on other salt marshes. General: Alaska, California, Greenland.

It is believed that this is purely an ecological form dependent upon the environmental conditions.

(25) *Enteromorpha nana* var. *marginata* (J. Ag.) comb.nov.

Newton, *Handb. Brit. Seaw.* p. 69, 1931; Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 257, 1920 (both as *E. marginata*).

Threads hairlike, 2–5 cm. long and up to 200μ wide, simple, free-living or attached, lax, contorted, occasionally with a few short proliferous branches; frond scarcely tubular, attenuate at base and apex, margins often inflexed; cells in rows, especially at the margins, 4–8μ dia., chloroplast filling the cell; membrane 16–20μ thick, cells 6–7μ high; colour bright green; adheres well to paper. (Fig. 63.)

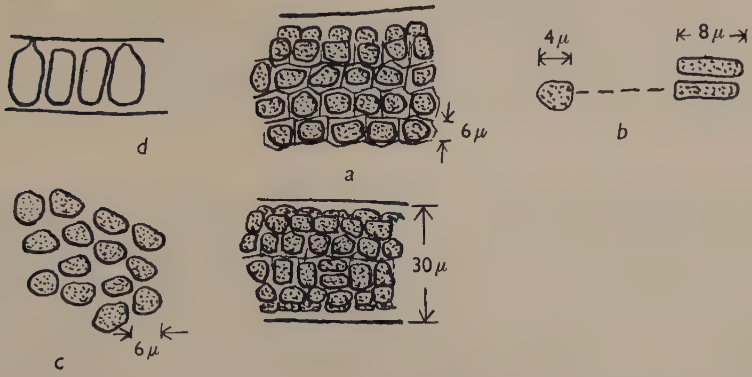


Fig. 63. *Enteromorpha nana* var. *marginata*: *a*, parts of thalli; *b*, cell variation; *c*, cells; *d*, membrane.

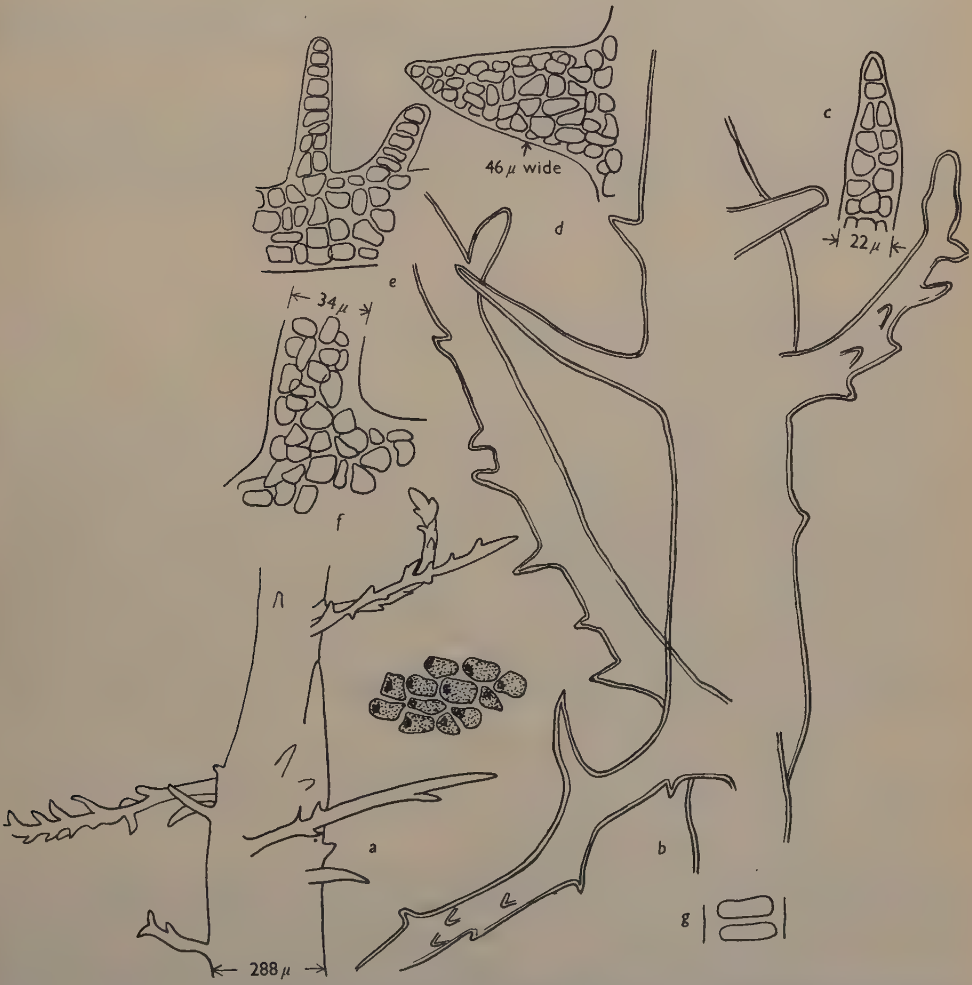


Fig. 64. *Enteromorpha ramulosa* f. *spinescens*: *a*, *b*, portions of thalli; *c*, *d*, apices of spiny outgrowths; *e*, proliferations; *f*, base of branch; *g*, membrane.

Distribution. Local: Narrow Neck, Shoal Bay (on mangrove leaves), Waiuku Creeks, Whareatea River, Port Elizabeth. General: Europe, Mediterranean, St Lawrence to Central Mexico, Vancouver to S. California.

There seems little justification for regarding this as a separate species.

(26) *Enteromorpha ramulosa* Hook. f. *spinescens* Kütz.

Kütz., *Tab. Phyc.* **6**, tab. 33, fig. 3*b*, 1856; Harv. in Hooker, *Fl. Nov. Zel.* **2**, 265, 1855; *Handb. N.Z. Flora*, p. 716, 1867; Laing, *Trans. N.Z. Inst.* **57**, 135, 1926 (as *E. ramulosa*); De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 86, 1923 (as *E. ramulosa*).

Plants up to 30 cm. long, membranous, subcartilaginous, rigid, setaceous, rough to the touch, often tangled into a mat, much branched, main thallus and branches bearing numerous spiny acuminate outgrowths; cells irregularly arranged, 4–20 × 5–24μ, 12–16μ high, 7–12μ wide in T.S.; chloroplast homogeneous, filling the cell; membrane 20–28μ wide, both walls up to 3μ thick; grass-green to pale green; adheres imperfectly to paper. (Fig. 64.)

Distribution. Local: Russell, Waitangi (B. of Is.), Seatoun, Nelson, Lyttelton, Blackhead, St Clair, Port Chalmers, Bluff, Caswell Sd. General: Arctic Europe and Asia, Atlantic (E. and W.), Mediterranean, W. Indies, Bolivia to Magellan Straits, Tasmania, Australia, Japan, Solomon Is., E. Indies.

Enteromorpha ramulosa is a widespread species which exists in a number of distinct forms, differing from each other primarily in size and density of the proliferations. The coarsest form is f. *robusta*, f. *spinescens* is rather less coarse, and f. *minor* is the finest. Hooker's records do not permit one to state which form of this variable species was recorded.

(27) *Enteromorpha ramulosa* f. *robusta* Le Jol.

Harv., *Phyc. Brit.* pl. 249, 1849–51 as *E. ramulosa*; Kütz., *Tab. Phyc.* **6**, tab. 33, fig. 2, 1856.

Plants up to 37 cm. long, much branched, firm, subcompressed, branches few to numerous, unequal in length; branches beset with branchlets and both covered with spinous outgrowths; cells large, irregularly arranged, 10–27μ dia., walls in older parts of the thallus thickened, chloroplast homogeneous, filling the cell; membrane 30–44μ thick; grass green, turning paler on drying; adheres poorly to paper. (Fig. 65.)

Distribution. Local: Tauranga, Oeo Beach, Lyall Bay, Wellington, Picton, Nelson, Collingwood River, Queen Charlotte Sd, Te Mahia, Te Papa, Pt Howard, St Clair, N. Heads (Otago), George Sd, Porirua. General: E. and W. Atlantic, N. Africa, W. Indies, Japan, Borneo, Celebes, New Guinea, Tasmania, Azores, Kerguelen, S. Africa.

The plant from Tauranga and another from Lyall's Bay were collected by Berggren and identified as *E. clathrata*. I have examined the specimens in herb. Univ. Lund and they clearly belong to this form.

(28) *Enteromorpha ramulosa* f. *minor* Kütz.

Kütz., *Tab. Phyc.* **6**, tab. 33, fig. 3*c*, 1856.

Frond lax, capillary, with elongated, subflaccid, diffuse branches which are beset with recurved branchlets; cells large, irregularly arranged, 12–32μ (average 20μ) dia., 19μ high in T.S., chloroplast homogeneous, wholly or almost filling the cell; membrane 28–32μ wide, both walls thickened up to 7μ; grass green; adheres imperfectly to paper. (Fig. 66.)

Distribution. Local: Raglan, Portobello, Pegasus (Stewart Is.), near H.W.M. General: Atlantic coasts of Europe, Spitzbergen, Mediterranean, Lower California, Australia.

(29) *Enteromorpha ramulosa* var. *acanthophora* (Kütz.) comb.nov.

Kütz., *Tab. Phyc.* **6**, tab. 34, fig. 1, 1856; Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 254, 1920; Laing, *Trans. N.Z. Inst.* **57**, 134, 1926 (all as *E. acanthophora*).

Plant subcoriaceous, up to 22 cm. long, tubulose, caulescent, consisting usually of a single main thallus up to 5 mm. wide, or with main branches arising at the base, increasingly virgate above, branches up to 2 mm. wide, curved, elongate or spiny, attenuate at base and apex, simple or bifurcating at the apex; cells 5·2–11·2μ (average 7·5μ) dia., 16μ high in T.S., cell walls thick, irregularly arranged in the main thallus and branches, in rows in the branchlets, chloroplast homogeneous, often only occupying part of the lumen; membrane 23–30μ thick in younger parts, 33–37μ in older, inner and outer walls up to 8μ thick; grass green; does not adhere well to paper. (Fig. 67, Pl. 34.)

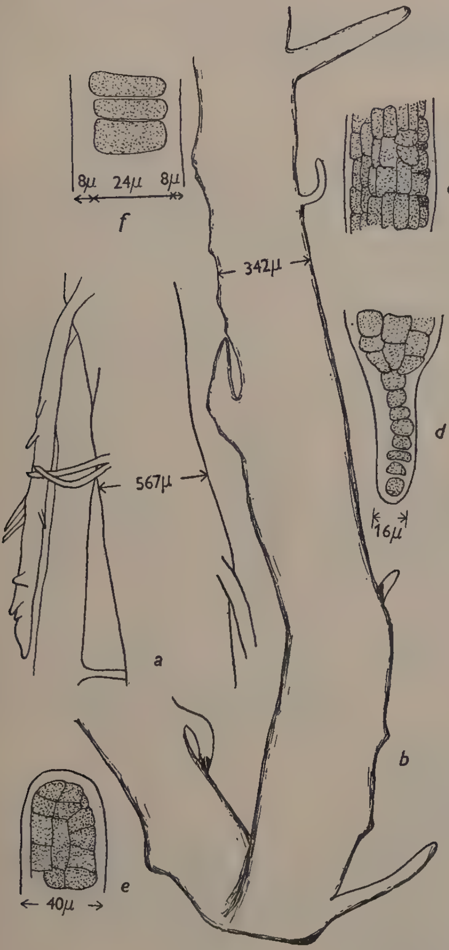


Fig. 65.

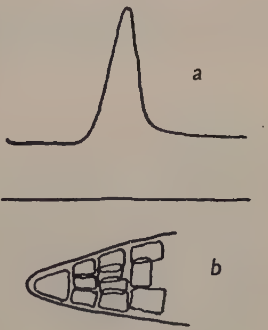


Fig. 66.

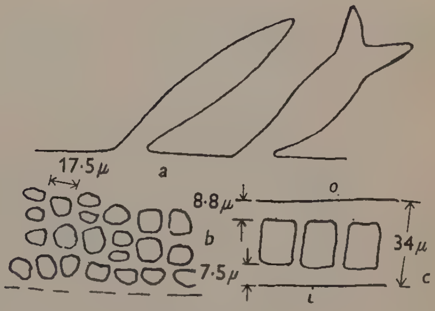


Fig. 67.

Fig. 65. *Enteromorpha ramulosa* f. *robusta*: *a*, *b*, portions of thalli; *c*, part of branch; *d*, *e*, apices of branches; *f*, membrane.

Fig. 66. *Enteromorpha ramulosa* f. *minor*: *a*, part of thallus; *b*, apex of spine.

Fig. 67. *Enteromorpha ramulosa* var. *acanthophora*: *a*, part of thallus showing outgrowths; *b*, cells; *c*, membrane. *i* = inner wall, *o* = outer wall.

Distribution. Local: Hobson's Bay, Wellington, Plimmerton, Nelson, Kaikoura, Tahuna, Waimakerere River, Akaroa, Oriental Bay, Cape Turnagain, Kena Beach, Moeraki, Bluff, Otago Harbour, St Clair, Stewart Is., Chatham Is., Porirua. General: S. California, Mexico, S. Australia, Tasmania.

It is possible that further study will show that this variety exists in two separate forms (Pl. 34) which may be seasonal, e.g. winter and summer. It is not always easy to distinguish it from other forms of *E. ramulosa*, but the row arrangement of cells in the branchlets and the attenuate bases of the branchlets appear to be good characters. There seems little justification for retaining this as a separate species.

(30) *Enteromorpha ramulosa* var. *acanthophora* ecad. **comosa** ecad.nov.

Plant up to 14 cm. long, main axis simple, profusely virgate, clothed with numerous short branches 5–8 mm. long, becoming shorter towards the apex of the main thallus, simple or bifurcate, with very short proliferations; cells and membrane as for the parent species, pale green; adheres moderately to paper. (Pl. 33.) Type specimen P.R.B. no. 23,611, Queen Charlotte Sd.

Distribution. Local: Queen Charlotte Sound. Endemic.

This form has been encountered only once and is probably the result of environmental conditions. In habit and appearance it is strongly reminiscent of *E. comosa* (J. Ag. mscr.) from Lake Constance at Geneva in Agardh's herbarium at Lund.

(31) *Enteromorpha clathrata* (Roth) Ag. var. *angustimembrana* Chapm.

Chapman, *J. Bot.*, *Lond.*, **78**, 263, 1940.

Thallus small, confervoid or with narrow branches up to 6 cm. long, tangled, up to 0·75 mm. wide, profusely branched especially at base; branches often composed of a few series of cells terminating in a monosiphonous portion; some branches short and spinelike, others with obtuse apices; cells arranged more or less in rows in the branches, irregularly arranged in main thallus; cells 14–18μ broad × 12–22μ long (average 16 × 18μ), rarely up to 40μ long in old parts of the thallus, 10μ high in T.S.; chloroplast granular, almost or wholly filling the cell; cell walls thick; membrane 18–24μ wide, outer wall 4–6μ thick, the inner 6–8μ; pale green in colour. (Fig. 68.)

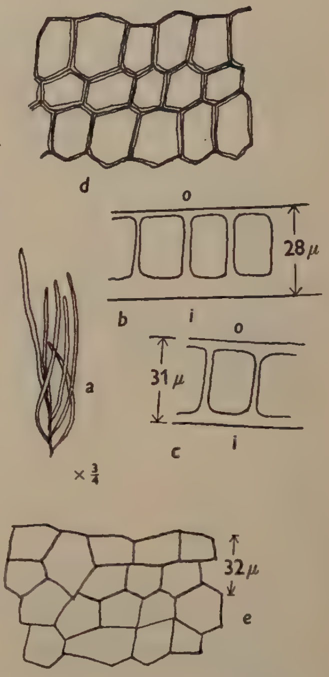


Fig. 68. *Enteromorpha clathrata* var. *angustimembrana*: *a*, plant; *b*, *c*, membrane; *d*, *e*, cells. *i* = inner wall, *o* = outer wall.

Distribution. Local: Rangihoua Bay Bluff, (Southland). General: South Africa.

Two specimens are referred doubtfully to this variety.

(32) *Enteromorpha clathrata* var. *plumosa* Kütz.

Harv., *Phyc. Brit.* pl. 263, 1849–51 (as *E. hopkirkii*); Kütz., *Tab. Phyc.* **6**, tab. 5, II, 1856 (as *Desmotrichum plumosum*); J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877 (*pro parte*).

Frond slender, hairlike, capillary, 10–15 (–30) cm. long, membranous, byssoid, much branched, flaccid; branches rarely opposite, feathery, not constricted at the base, erect, attenuated at apex, beset with minute subulate ramuli; ultimate ramuli monosiphonous all branches terminating in a single series of cells; cells large, hyaline, subrectangular, not elongated at base of branch, arranged in longitudinal and often transverse series in axis and major branches; cells 15–32μ × 16–60μ long in axis, 15–25μ dia. in branches; chloroplast granular, not filling the cell; membrane 24–28μ wide; pale yellowish or bright green, becoming paler on drying. (Fig. 69.)

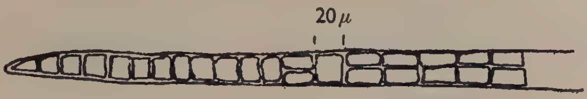


Fig. 69. *Enteromorpha clathrata* var. *plumosa*: monosiphonous branch apex.

Distribution. Local: Rangitoto, Lake Forsyth, Otago Harbour, Stewart Is. (Lyall Bay, Tauranga, Otago, Bluff?). General: Atlantic coasts of Europe and the U.S.A., Mediterranean, Red Sea (?), East Indies, Philippines, China, Japan, Kurile Is., Tonga, Samoa, S. Australia, S. Orkneys, S. Africa, W. Indies, Vancouver to lower California.

Hooker (1867) also records *E. erecta* (*E. clathrata* var. *erecta*) from the Auckland Is., but no specimens of this characteristic species exist in the various herbaria and the form is therefore omitted in this list.

J. Agardh (1877) records *E. clathrata* from Otago, Bluff, Lyall Bay and Tauranga. No plants of this species have been encountered, and it is likely that some of the records at least probably refer to the present form.

(33) *Enteromorpha clathrata* var. *pumila* (Aresch.) comb.nov.

Schiffner, *Hedwigia*, **71**, p. 190, 1931 (as *E. chartacea* f. *minor*).

Plants 4–6 cm. long, up to 3 mm. broad, caespitose, much branched at the base, branches attenuate at base, flattening and dilating above, subcompressed or tubular; cells in rows in small branches, less distinctly so in larger branches, 10–24μ (average 17μ) dia., 9–30μ high in T.S., elongated at base of the branches, chloroplast granular, not filling the cell; membrane 12–42μ thick, both walls slightly thickened, the inner more than the outer; pale green in colour; adheres imperfectly to paper. (Fig. 70.)

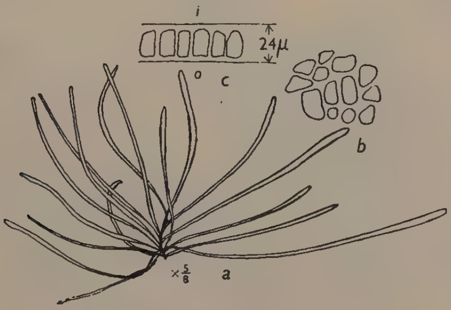


Fig. 70. *Enteromorpha clathrata* var. *pumila*: *a*, plant; *b*, cells; *c*, membrane. *i* = inner wall, *o* = outer wall.

Distribution. Local: Kermadecs, Russell (Moturoa), Greymouth. General: Europe, Adriatic, Madeira, Red Sea, Ceylon, Australia, S. California, Gold Coast, Jamaica.

(34) *Enteromorpha clathrata* ecad *prostrata* Le Jol.

Chapman, *J. Linn. Soc.* (*Bot.*), p. 205, 1937; Newton, *Handb. Brit. Seaw.* p. 68, 1931.

Thallus prostrate, up to 30 cm. long (usually much less), 1–8 mm. dia., tangled, contorted, much and repeatedly branched, tubular; irregularly inflated, often crispate, branches tapering to the apex, often spinous; cells large, in rows in the branches, not so in main thallus, 8–28μ dia., chloroplast granular, not filling the cell; membrane 17–50μ wide, the outer wall much thickened; pale green or grass green; does not adhere to paper. (Fig. 71.) V.W.L. 303.

Distribution. Local: Waitangi River (B. of Is.) Hooper's Inlet and probably elsewhere. General: Iceland, Great Britain, France, Denmark, New England (U.S.A.), Adelaide (S. Australia).

This form is typical of salt marsh and brackish conditions and is always free-living.

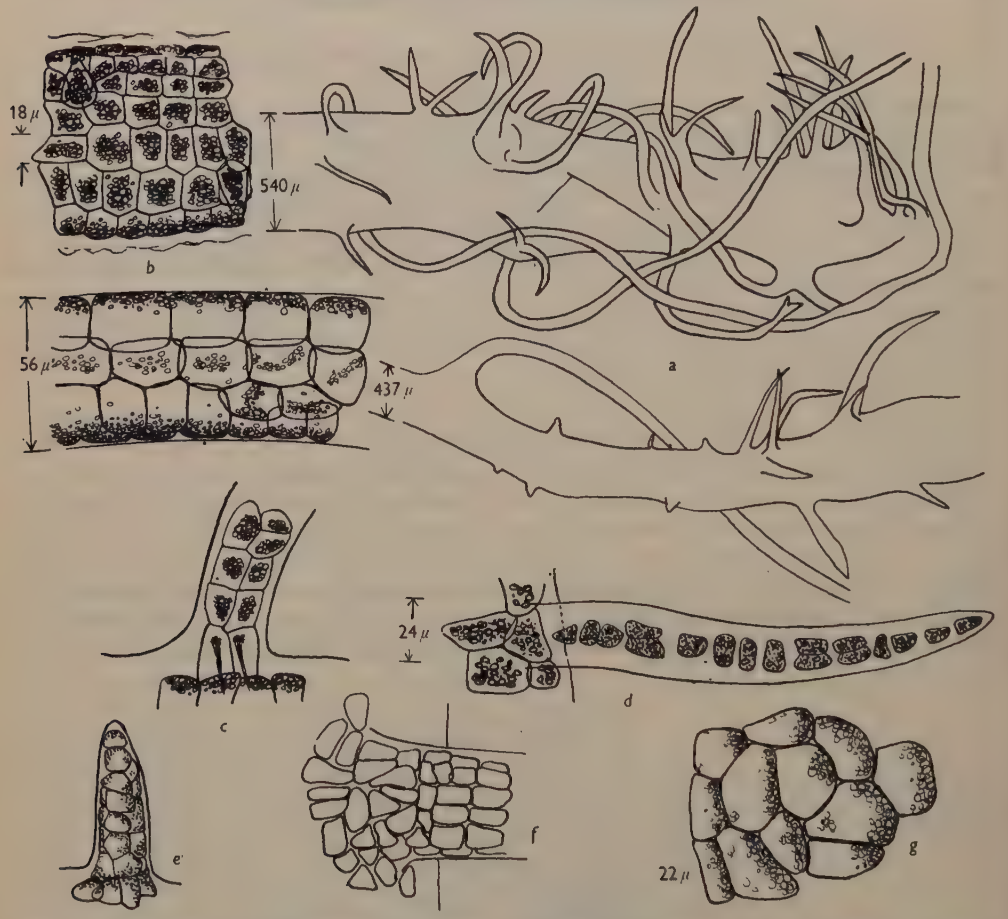


Fig. 71. *Enteromorpha clathrata* ecad *prostrata*: *a*, portions of thalli; *b*, ditto, enlarged; *c*, base of branchlet; *d*, branchlet; *e*, spine; *f*, base of branch; *g*, cells.

(35) *Enteromorpha clathrata* var. *usneoides* (Bonnem.) comb.nov.

J. Ag., *Till Alg. Syst.* **6**, p. 157, 1882; Newton, *Handb. Brit. Seaw.* p. 72, 1931 (both as *E. usneoides*).

Plants up to 30 cm. long, ectocarpoid in habit, cylindrical, tubular; branches mostly setaceous, ramuli spreading, attenuate at base and apex, cells rotundo-angulate, irregularly arranged in axis and branches, in rows in branchlets, 8–33μ dia. 16–20μ high in T.S., walls thick, chloroplast granular, almost filling the cell; membrane 20–32μ thick, outer wall slightly thickened; plants dark or grey-green, paler on drying; adheres moderately to paper. (Fig. 72.)

Distribution. Local: Charteris Bay (drift). General: Europe, Connecticut, Adelaide (S. Australia) and probably elsewhere.

One plant appeared to be referable to this variety, which has not been well understood in the past.

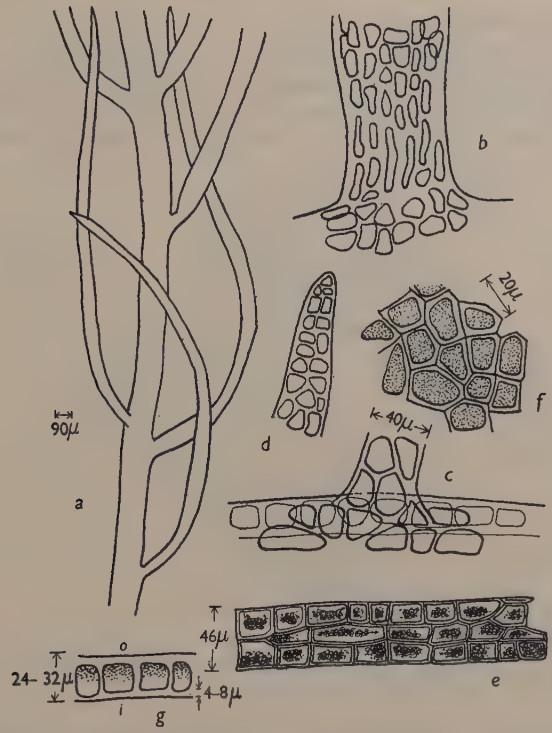


Fig. 72. *Enteromorpha clathrata* var. *usneoides*: *a*, part of plant; *b*, base of branch; *c*, base of branchlet; *d*, apex of branch; *e*, cells of branch; *f*, cells of main axis; *g*, membrane. *i* = inner wall, *o* = outer wall.

(36) *Enteromorpha clathrata* var. *ralfsii* (Harv.) comb.nov.

Harv., *Phyc. Brit.* pl. 282, 1849–51; Newton, *Handb. Brit. Seaw.* p. 68, 1931 (both as *E. ralfsii*).

Fronds tubular or almost solid, 30–80μ wide, flexuose, densely aggregate, capillary, simple or with a few short spine-like ramuli; cells large, hyaline, giving the thallus a reticulate appearance; 3–6 rows of cells in the frond, cells 10–20μ dia., chloroplast not filling the cell; yellow or grass green; adheres well to paper. (Fig. 73.)

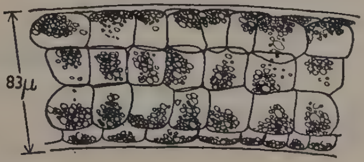


Fig. 73. *Enteromorpha clathrata* var. *ralfsii*.

Distribution. Local: Piha, Poverty Bay, Grassmere Lagoon, Portobello. General: Europe, probably elsewhere.

This form is easily overlooked and can also be confused with *E. prolifera* var. *torta*, from which it differs in the granular nature of the plastid and the fact that the plastid does not fill the cell. It represents the ultimate reduction in the *E. clathrata* series.

(37) **Enteromorpha crassimembrana** sp.nov.

Thallo simplici, capillari, paulatim in stipitem attenuato, lineari, 4–5 cm. longo; cellulis irregulariter dispositis, 10–26μ dia., plerumque 14–18μ, 5.5–13μ altis in T.S.; parietibus primum tenuibus, deinde valde crassis; membrana 35–60μ crassa, pariete interiore valde crassato et lamellato, pariete exteriore 5–9μ crasso, colore vepallido, paene albo.

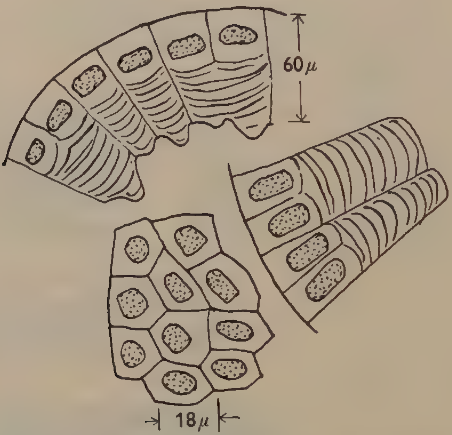


Fig. 74. *Enteromorpha crassimembrana*: cells and membrane.

Thallus simple, capillary, attenuate gradually at the stipe, linear, 4–5 cm. long; cells irregularly arranged, 10–26μ (average 14–18μ) dia., 5·5–13μ high in T.S.; walls thin at first, later becoming very thick; membrane 35–60μ thick, inner wall much thickened and lamellate, outer wall 5–9μ thick, very pale, almost white; adheres imperfectly to paper. (Fig. 74.)

Type specimen in Herb. Auk. Inst.; Co-type in herb V. W. Lindauer. Cape Maria.

Distribution. Local: Cape Maria. Endemic.

This is a very remarkable species, especially in the thickness of the membrane. In T.S. the tube is almost solid because of the thick inner wall. The cells appear almost to be in pairs in segments (Fig. 74). Taxonomically it appears to be related to *E. procera*, especially f. *eramosa*.

(38) *Enteromorpha procera* Ahln. f. *minuta* Chapm.

Chapman, *J. Bot., Lond.*, 78, 265, 1940.

Thallus narrow, tubular, linear, branched at the base, branches more or less attenuate at bases; branches 1·5–2 cm. high, 1–3 mm. wide; cells in youngest parts in rows, row arrangement not distinct in older parts; cells 15–18μ dia., 14–32μ long × 14–22μ wide; chloroplast filling the cell; membrane 25–28μ wide, inner wall slightly thickened. V.W.L. 108.

Distribution. Local: Bay of Islands on *Schizymenia* and *Carpophyllum*, Whangaparaoa Hds., Piha, Howick, St Heliers, Narrow Neck, Oneroa, Pinnacles, Fletcher's Bay, Whitianga, Aurere Bay on *Corallina*, Porirua. General: Java, S. Africa, S. Australia, Jamaica.

(39) *Enteromorpha procera* f. *novaezelandiae* Chapm.

Chapman, *J. Bot., Lond.*, 78, 265, 1940.

Plants small, up to 2 cm. long, tubular, densely branched at base, branches rare above; branching alternate, rarely opposite, branches attenuate at base; tertiary branches terminating in a monosiphonous portion, primary branches obtuse, not monosiphonous; cells in rows, 12–22μ (average 16–20μ) dia., 15–17μ high in T.S.; chloroplast homogeneous, filling the cell; membrane 20–24μ, slightly thickened on both sides; light green in colour; usually epiphytic. (Fig. 76.)

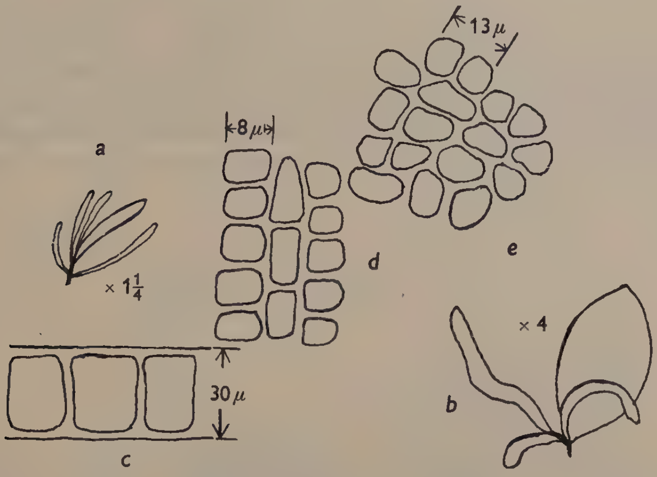


Fig. 75. *Enteromorpha procera* f. *minuta*: *a*, *b*, plants; *c*, membrane; *d*, cells near base of branch; *e*, cells of expanded distal region.

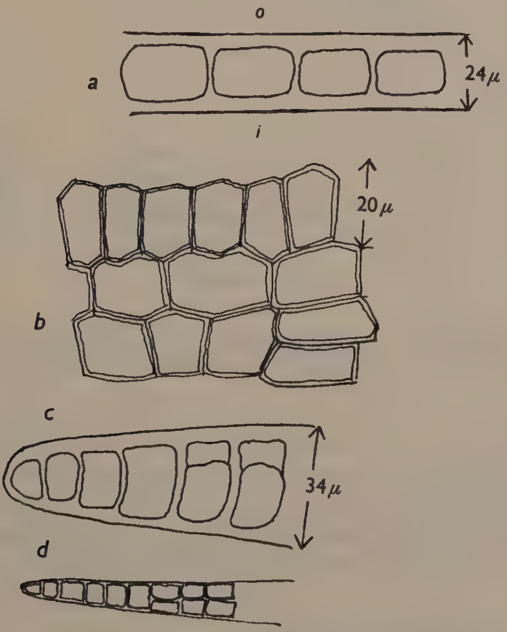


Fig. 76. *Enteromorpha procera* f. *novaezelandiae*: *a*, membrane; *b*, cells; *c*, *d*, apices of branches. *i*=inner wall, *o*=outer wall.

Distribution. Local: Bay of Islands (on *Hormosira*, *Scytothamnus*, *Splachnidium*), Taranga Is. (on *Ecklonia*), Leigh, Orewa, Stanmore Bay, Pt. Fitzroy, Mairangi, St Heliers, Narrow Neck, Gannet Rock, Noises, Te Puru, Raukura Pt., Fletcher's Bay, Nelson, Lyttelton (on *Corallina*). Endemic.

(40) *Enteromorpha procera* f. *chlorotica* (J. Ag.) comb.nov.

J. Ag., *Till Alg. Syst.* **6**, p. 136, 1882; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 85, 1923 (as *E. chlorotica*).

Thallus small, 6–9 cm. long, branched mainly from the base, membranaceous; branches attenuate at base but dilating above and becoming cuneate with an undulate margin; chloroplast homogeneous; cells 11·2μ average dia., 13–16μ tall in T.S., cell walls very thick; membrane 18·5–24μ thick, inner walls 5–7μ thick; plants pale green; adheres moderately to paper. (Fig. 77 I.)

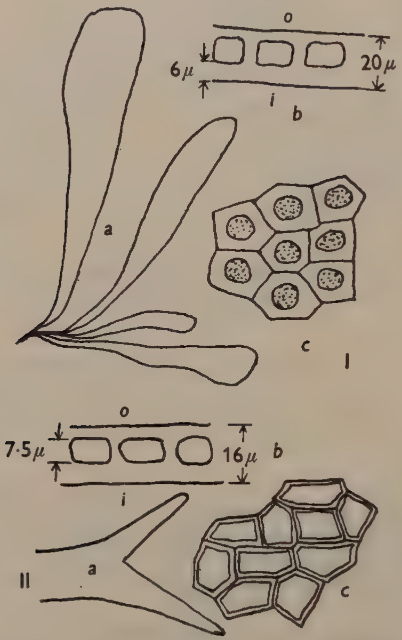


Fig. 77. I. *Enteromorpha procera* f. *chlorotica*: *a*, plant; *b*, membrane; *c*, cells. II. *E. procera* var. *prolifica*: *a*, apex of proliferation; *b*, membrane; *c*, cells. *i* = inner wall, *o* = outer wall.

Distribution. Local: Kermadecs, Lyall Bay. General: Malaya.

This differs from the other forms of *E. procera* in the extreme paleness of the plants.

(41) *Enteromorpha procera* var. *prolifica* Chapm.

Chapman, *J. Bot., Lond.*, **78**, 264, 1940.

Adult thallus large, up to 22·5 cm. long and 8 mm. broad, simple or branched, much proliferated, branches and proliferations slightly attenuate at the base, tubular or collapsed; cells of the older part 8–26μ (average 14–16μ) dia., 18–22μ high in T.S., chloroplast homogeneous except in the cells of the stipe; membrane 20–36μ wide, the inner wall up to 8μ thick; plants green or pale green; adheres well to paper. (Fig. 77 II.)

Distribution. Local: Bay of Islands, Plimmerton, Karetane, Brighton, Kaikoura (?), Chatham Is. (?). General: California, Norway.

Plants from the Chatham Is. and Kaikoura are included here with some reservation as they were not quite typical.

(42) *Enteromorpha procera* f. *denudata* (Ahln.) comb.nov.

Hylmö, Stud. Grünalg. p. 15, pl. 1, fig. 14, pl. 2, fig. 10, 1916 (as *E. denudata* Ahln).

Thallus up to 24 cm. long and 3 mm. wide, delicate, elongate, much branched, axis and branches constricted at intervals, axis dilating from a narrow stipe, branches simple or with fine hair-like branchlets, constricted at the base and attenuate at the apex; cells irregularly arranged in the main axis, in rows in the branches 13–33μ dia., average 22μ, walls thick; membrane 16–24μ wide, inner wall not thickened; adheres well to paper. (Fig. 78.)

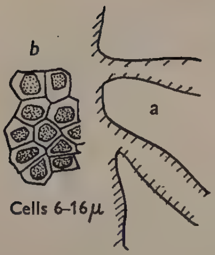


Fig. 78.

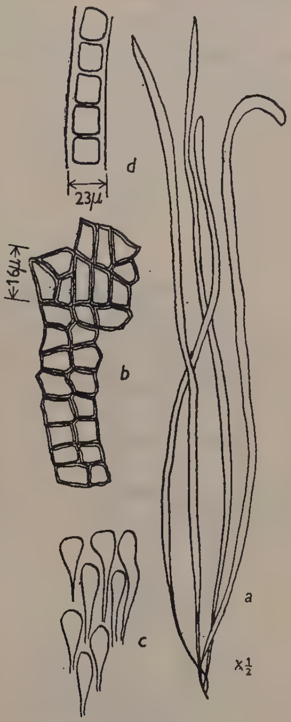


Fig. 79.

Fig. 78. *Enteromorpha procera* f. *denudata*: *a*, base of branches; *b*, cells.

Fig. 79. *Enteromorpha procera* f. *eramosa*: *a*, plant; *b*, cells of upper part of branch; *c*, cells of base of branch; *d*, membrane.

Distribution. Local: Picton. General: Europe, Falkland Is., Japan, Rio de Janeiro, S. Australia.

The one specimen seen agreed well in its characters. It is probably more widespread in New Zealand than this one record suggests.

(43) *Enteromorpha procera* f. *eramosa* (Schiff. MS.) comb.nov.

Plants filiform, up to 40 cm. long and 1 cm. wide, branched only at the base; branches simple, dilating from a narrow base, tubular or compressed; cells elongated at the base of the branches, arranged more or less in rows, row arrangement sometimes obscure, cells

7–20μ dia., average 10–12μ, chloroplast homogeneous, filling the cell; membrane 23μ thick above, 37μ near base; plants pale yellow-green; adheres well to paper. (Fig. 79.)

Distribution. Local: Port Fitzroy, Cape Runaway, Wellington (Lyall Bay, Titahi Bay), Hooper's Inlet, St Clair. General: Great Britain, Algiers, New England (U.S.A.), Australia, Falkland Is.

(44) *Enteromorpha procera* f. *subundulata* (Schiffn.) comb.nov.

Schiffner, *Hedwigia*, 71, 190, 1931, as *E. prolifera* f. *subundulata.*

Thallus elongated, tubular or collapsing, 10–15 cm. long, up to 3 mm. wide, simple or branched, branches hair-like, arising from a broad base with obtuse apices; cells irregularly arranged, thick-walled, some row arrangement evident in smaller branches, 8–27μ (average 15μ) dia., chloroplast homogeneous, filling the cell; membrane 15–24μ wide, inner wall up to 6μ thick, outer wall 1·5–4·5μ thick; pale golden green; adheres moderately to paper. (Fig. 80.)

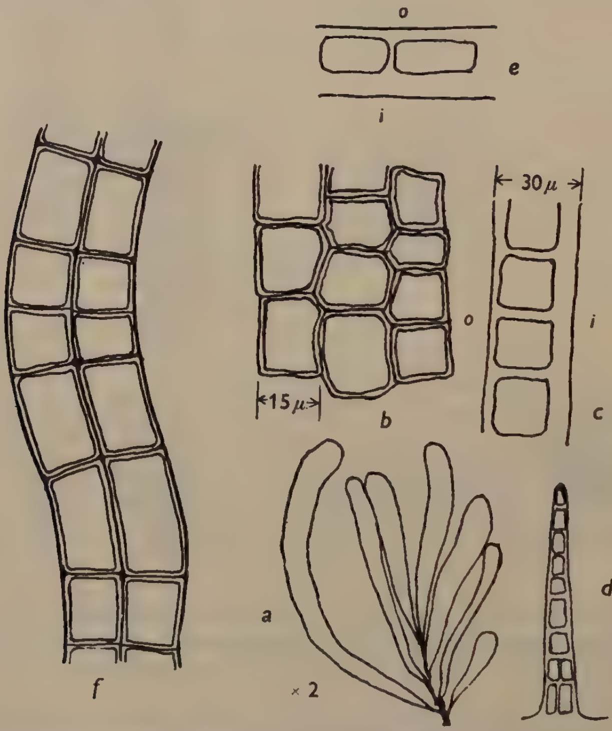


Fig. 80. *a–d, Enteromorpha procera* f. *opposita*: *a*, plant; *b*, cells; *c*, membrane; *d*, apex of a branchlet. *e, E. procera* f. *subundulata*: membrane. *f, E. percursa.*

Distribution. Local: Scott's Point, Bluff (90 Mile Beach). General: Europe, Mediterranean, Ceylon, Tasmania, Alaska, Valparaiso, Nova Scotia.

The thick walls and the membrane place this form nearer to *E. procera* than *E. prolifera.* Schiffner's exsiccata no. 449 is typical. Plants occur in herbaria labelled variously as forms of *E. compressa* and *E. prolifera.*

(45) *Enteromorpha procera* f. *opposita* (J. Ag. MS.) comb.nov.

Thallus 4–16 mm. wide, dilating from a narrow stipe, often branched considerably near the base, less so further up; branches commonly opposite, in pairs, dilating from a constricted base, obtuse at the apex; filiform branchlets may also be present; cells arranged in rows in the branches, row arrangement obscured in the main thallus, 8–24μ dia. in main axis, 13–15μ long × 6–14μ wide in branches, 11μ high in T.S.; membrane 21–30μ wide, inner wall up to 7·5μ thick, the outer about 3μ; plants pale green; adheres imperfectly to paper. (Fig. 80.) V.W.L. 155 as *E. procera* f. *subnuda.*

DISTRIBUTION. Local: Russell. General: Scandinavia, Mediterranean, S. Africa, Gold Coast, California, Tongatabu.

Considerable care is required in distinguishing between the three forms just described. It is possible that they should all be included within a single form, but when fully developed they appear to be quite characteristic.

(46) *Enteromorpha percursa* (C. Ag.) J. Ag.

Collins, Green Alg. N. Amer. p. 197, 1909; Newton, *Handb. Brit. Seaw.* p. 76, 1931 (as *Percursaria percursa*).

Plant filiform, simple, up to several cm. long, flexuose, twisted; filaments usually composed of two rows of cells, sometimes of one row, the cells of the two rows usually opposite; cells 10–15μ, 1–2 times as long as broad. Walls rather thick. (Fig. 80*f*.)

DISTRIBUTION. Local: Grassmere lagoon. General: Europe, N. America and probably elsewhere.

It is surprising that this plant has not been recorded before in New Zealand. It probably occurs elsewhere on salt marshes in the South Island.

Many workers place it in a separate genus (*Percursaria*) but I believe it is simply an extreme reduction form of the *Enteromorpha* type. Laing (1926) records *E. percursa* var. *ramosa* from Dunedin but there is no material in his herbarium (see Naylor, 1954, p. 663).

CAPSOSIPHONACEAE

Frond membranaceous, tubular, with wall of a single layer of cells, attached by a disk; cells uninucleate with a single chloroplast, arranged in twos and fours in distinct longitudinal series; reproduction by aplanospores.

Capsosiphon Gobi

Plants filamentous, hollow, gelatinous, the cells mostly in twos and fours, sometimes enclosed with the walls of the mother cell, arranged in distinct longitudinal series, the series loosely connected laterally.

Capsosiphon aurea Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 54, 1952.

Plants filamentous, tubular, up to 4 cm. long, 2·5 mm. wide, brown or golden in colour, attached by a basal disk; cells in twos and fours, arranged in longitudinal and horizontal series, groups of the longitudinal series loosely connected; vegetative cells 5·5–11·2μ dia., reproductive cells 11·2–13μ dia., cells in young filaments usually in pairs, sometimes elongate, 3·75 × 7·5μ long; membrane 15–21μ wide, cells 7·5–11·2μ dia., more or less spherical; reproduction by ?aplanospores, 8 per cell. (Fig. 81.)

DISTRIBUTION. Local: Russell (Bay of Islands). Endemic.

This plant is extremely interesting because it is clearly a *Capsosiphon*, yet it differs in certain important respects from *C. fulvescens*, the only other known species. In *C. fulvescens* the pairs of cells are retained within the sheath of the parent cell in a *Gloeocapsa*-like form. In *C. aurea* there is no distinct parent mother cell sheath. Both species are tubular, lubricous and with the longitudinal series of cells loosely connected. In *C. fulvescens* each row of cells separates, in *C. aurea* several rows separate together. Except for its tubular nature, the construction of *C. aurea* is very akin to that of a

Prasiola; members of the genus *Prasiola* are always flat plates, whereas *Capsosiphon* is tubular.

Ecologically *C. fulvescens* and *C. aurea* are similar because both are found in streams where the plants are subjected to tidal influence twice daily. The salinity will generally be low and there may also be pollution (Waern, 1952).

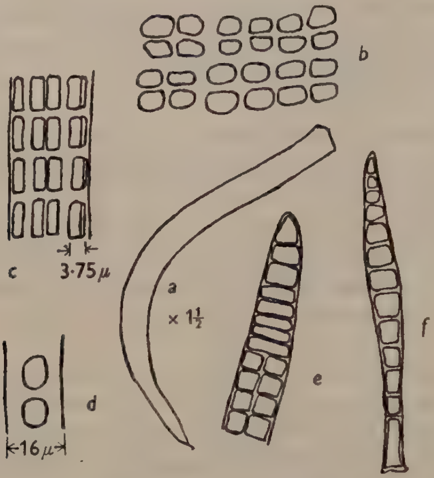


Fig. 81. *Capsosiphon aurea*: *a*, plant; *b*, cells of old thallus; *c*, cells of young branch; *d*, membrane; *e*, apex of young branch; *f*, plantling.

PRASIOLACEAE

Filamentous or membranaceous; cells with stellate chloroplast and one pyrenoid; asexual reproduction by segmentation of the frond, by akinetes and by aplanospores; sexual reproduction unknown.

Prasiola Menegh.

Frond membranaceous, monostromatic, attached by short filiform prolongations, by the edge of the membrane or by a thickened stipe; cells with stellate, axile chromatophore and one pyrenoid, dividing to form groups of fours; these groups forming similar larger groups, the spaces between the groups of various orders constituting narrower or wider spaces, running in definite directions through the frond; vegetative reproduction by fragmentation; asexual reproduction by akinetes or aplanospores.

1. Thallus subrotund, crenulate. *P. antarctica*
   Thallus filamentous or a flat expanded membrane. 2
2. Thallus filamentous, stipitate, expanding to a linear membrane. 3
   Thallus a flat expanded membrane, non-stipitate, without rhizoids. *P. snareana*
3. Thallus free or attached by a few short rhizoids. *P. crispa*
   Thallus attached by an expanded attachment disk. *P. stipitata*

There are probably more species of *Prasiola* to be found in New Zealand, but a full understanding of the present species will not be possible until the seasonal forms and developmental stages have been fully studied.

(1) *Prasiola antarctica* Kütz.

Kütz., *Tab. Phyc.* 5, t. 40, f. 4, 1855; Hooker, *Flor. Antarct.* 2, p. 498 nec alior as *Ulva crispa*, 1847; Harv. in Hooker, *Fl. Nov. Zel.* 2, 265, 1855; *Handb. N.Z. Flora*, p. 715, 1867.

Thallus commonly small, 3–4 mm. long, 2–3 mm. wide, occasionally enlarging up to

2 cm. dia., subrotund or oblong; margin irregularly subcrenulate; cells 4–10μ (average 6μ) dia.; membrane 15–16μ wide, cells 8·25–8·8μ high, loosely disposed in twos and fours. (Fig. 82.)

Distribution. Local: Wardell's Creek. General: Antarctic seas.

Specimens collected by Mr Lindauer clearly belonged to this species, but some of the plants are larger than would be expected from the original description.

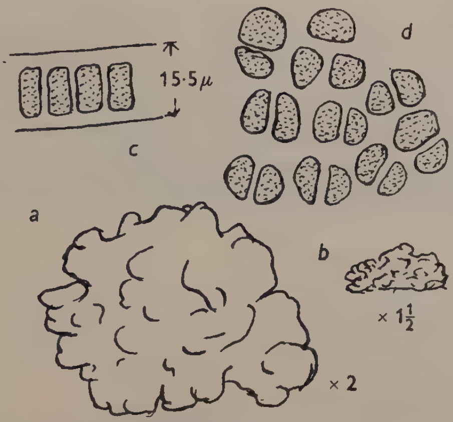


Fig. 82. *Prasiola antarctica*: *a*, *b*, plants; *c*, membrane; *d*, cells.

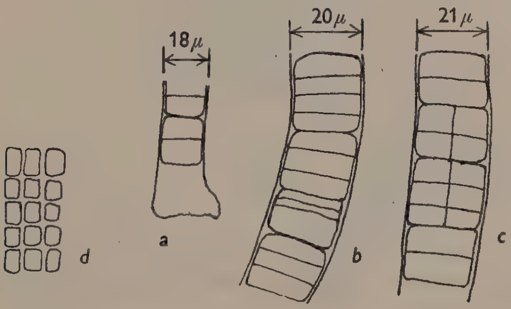


Fig. 83. *a–c*, *Prasiola crispa*: '*Hormidium*'-stage: *a*, base; *b*, *c*, parts of filaments. *d*, *P. snareana*: cell arrangement.

(2) *Prasiola crispa* Menegh.

Newton, *Handb. Brit. Seaw.* p. 79, 1931.

Plant forming an expanded flattened thallus, free or attached by a few short rhizoids; under certain conditions thallus existing as a single row of cells, 18·5–22μ wide, in groups of twos, threes and fours, cells much shorter than broad (*Hormidium*-stage) or as a filament with a few longitudinal divisions (*Schizogonium*-stage); cells of expanded thallus 3–13μ thick. (Fig. 83.)

Distribution. Local: Mercury Bay (Coromandel) in cracks in the rock in spray zone, Green Is. (Otago), Headland Pt. (Portobello). General: Europe, N. America.

The plants were mainly in the *Hormidium* stage but there were typical expanded thalli.

(3) **Prasiola snareana** sp.nov.

Thallus usque ad 1·5 cm. longa, 0·6 cm. lata, delicatissima, non stipitis, expansis; membrana 5–8μ lata; cellulae ordinatae 4–7·5μ latae, 8·2–11μ longae.

Thallus up to 1·5 cm. long and 0·6 cm. wide, very thin, delicate, non-stipitate, expanded; membrane 5–8μ thick; cells in rows, 4–7·5μ wide × 8·2–11μ long; adheres well to paper. (Fig. 83.) Type specimen 32, in Herb. Laing, Snares.

Distribution. Local: Snares Is. Endemic.

This plant is very similar to the expanded portions of *P. crispa*, but there is no stipe portion nor are rhizoids present.

(4) *Prasiola stipitata* Suhr

Newton, *Handb. Brit. Seaw.* p. 79, fig. 58, 1931; Taylor, *Mar. Alg. N.E. N. Amer.* p. 76, pl. 1, figs. 4–7, 1937.

Plants tufted, forming a low mat or in cracks, dark green; single plants small, up to 6 mm. long, base narrowed to a stipe portion, expanding above to fan or kidney shape, 10–14μ thick, apex obtuse, margins often incurled; cells 3–7·3μ arranged in rows, in expanded part crowded into blocks; akinetes formed in expanded portion, 10–12μ dia. (Fig. 84.)

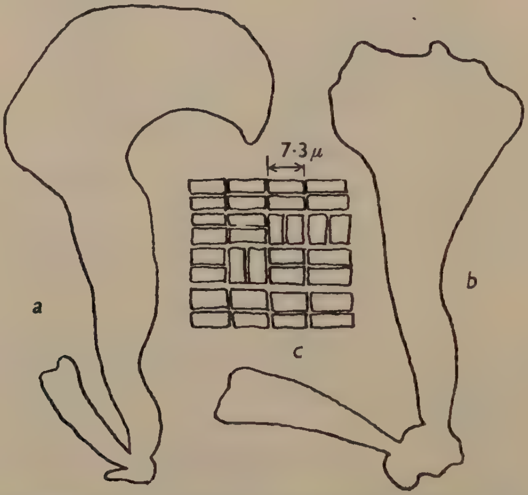


Fig. 84. *Prasiola stipitata*: *a*, *b*, plants; *c*, cells in expanded part. (*a* × 990; *b* × 720.)

Distribution. Local: Gannet Rock. General: Europe, Massachusetts.

The material agreed in all respects with the above description. The marked discontinuity is a major problem, but in view of the association of the species with birds this problem may be more apparent than real.

CHAETOPHORALES

Filamentous, heterotrichous with prostrate and erect systems, though latter often reduced and former present as a pseudoparenchymatous disk; hairs of diverse kinds usually present; reproduction by asexual zoospores or isogametes.

CHAETOPHORACEAE

Fronds filamentous except in a few doubtful forms, usually much branched, sometimes united in disk-like expansions; cells uninucleate, with band- or disk-like chloroplast usually with one pyrenoid; hairs often present, varying in character; asexual reproduction by 2- or 4-ciliate micro- and macrozoospores, by aplanospores or akinetes; sexual reproduction by 2-ciliate isogametes, more rarely anisogametes.

1.	Primary filaments creeping, producing distinct erect filaments.	5
	No distinctive erect filaments.	2
2.	Thallus an epiphytic disk-like structure.	4
	Thallus endophytic or in shells of molluscs.	3
3.	In the cell walls of various algae or in remains of phanerogams.	*Entocladia*
	In the calcareous shells of living or dead molluscs.	*Gomontia*
4.	Pyrenoids present in the cells.	*Protoderma*
	Pyrenoids absent.	*Ulvella*
5.	Sporangia on erect filaments only.	*Pilinia*
	Sporangia on prostrate and erect filaments.	*Sporocladopsis*

Sporocladopsis Nasr

Plant filamentous, with erect and prostrate filaments; uninucleate with single parietal chloroplast and few pyrenoids; reproduction by zoospores produced in distinct sporangia.

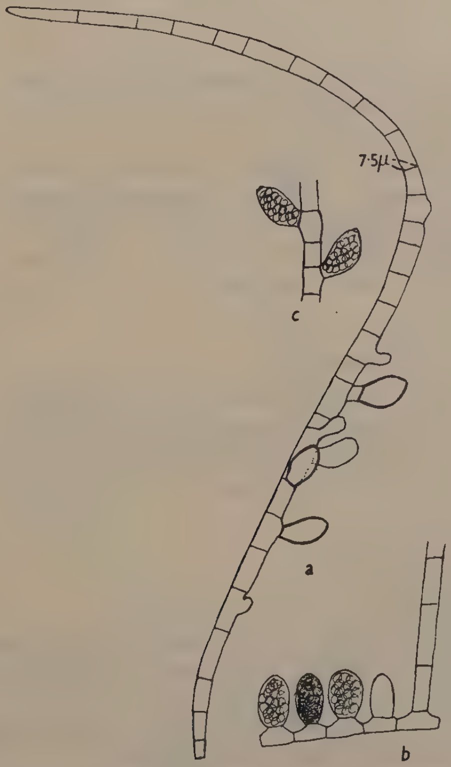


Fig. 85. *Sporocladopsis novaezelandiae*: *a*, erect aerial filament; *b*, prostrate filament with sporangia; *c*, ripe sporangia with apical pores. (After Chapman.)

Sporocladopsis novaezelandiae Chapm.

Chapman, *Farlowia*, **3** (4), 496, fig. 4, 1949.

Plants minute, epiphytic, consisting of a prostrate layer one cell thick from which simple, erect filaments arise; filaments up to 40 cells long (average 20–25 cells), cells 5·5–7·5μ wide; $1\frac{1}{2}$–$2\frac{1}{2}$ times as long as broad; sporangia sessile or borne on a unicellular stalk, distributed over the entire prostrate thallus or borne more or less secundly on the erect filaments or terminally, 9·3–11·3μ wide, 17–22·5μ long, dehiscing by an apical pore. (Fig. 85.) V.W.L. 308.

Distribution. Local: Russell, Bay of Islands on *Ecklonia* and *Schizymenia*, Lyall Bay, Kaikoura on *Lessonia*, Narrow Neck on *Carpophyllum*, Anawhata on *Durvillea*, Oneroa, Pohutakawa Flat, Oruawharo Bay. General: Queensland.

Nasr (1947) placed this genus in the Trentepohliaceae, but there is no evidence of haematochrome, and it would seem that in view of the aquatic habitat of the known species that the genus is more properly placed in the Chaetophoraceae.

Ulvella Crouan

Thallus forming a small disk upon larger plants, firmly attached by the under surface, monostromatic at first, later polystromatic, composed of radiating, laterally-united, dichotomously-branched filaments; cells without pyrenoids; reproduction by 2-ciliate zoospores.

Ulvella lens Crouan

Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 295, pl. 33, 1920.

Thallus orbicular, epiphytic, bright green, up to 1·5 mm. dia.; marginal cells usually cuneate, 3·5–4·5μ dia., 15–25μ long; central cells 8–15μ dia. (Fig. 86.)

Distribution. Local: Epiphytic on *Enteromorpha lingulata*, Wycliffe Bay, on *E. compressa*, Lyall Bay. General: Europe, North America, Pacific North America.

The specimens agreed very closely with the description and figure provided by Setchell & Gardner.

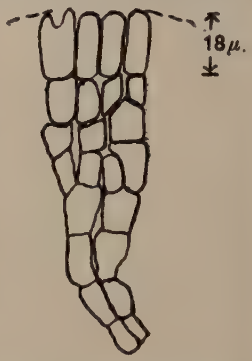


Fig. 86. *Ulvella lens*: part of thallus.

Protoderma Kütz.

Frond a minute disk, closely appressed to the substrate, formed initially of radiating branched filaments, which, except at the margin, form a subparenchymatous disk one or more cells thick; chloroplast parietal, disk-like, with one pyrenoid; asexual reproduction by aplanospores and by biciliate zoospores.

Protoderma marina Reinke

Newton, *Handb. Brit. Seaw.* p. 66, fig. 52, 1931.

Plants forming thin coatings of irregular shape; thallus consisting of parenchyma-like cells, 6–12μ dia., irregularly placed except at the margin where they are in rather indistinct radiating series.

Distribution. Local: On *Polysiphonia* Narrow Neck, on shells Manakau Harbour, on stones, Lyttelton. General: Europe, New England.

This species usually occurs on stones, but the plants on the *Polysiphonia* appeared to be quite characteristic. Newton (1931) places this genus in the Ulvaceae, but it would appear that a more correct position would be in the Chaetophoraceae, because it is apparently closely allied to *Ulvella* and other allied genera.

Entocladia Reinke

Plants microscopic, creeping on or within other algae and aquatic plants, composed of irregularly branched filaments without hairs; growth mostly by division of terminal cells; chloroplast parietal with one or more pyrenoids; reproduction by 2–4 ciliate zoospores produced 4 or more in a cell.

In this account the concept of the genus as given by Setchell & Gardner (1920) is adopted. This is rather more restricted than that accepted by Collins (1909).

1.	In *Rivularia atra.*	*E. rivulariae*
	In other hosts.	2
2.	Filaments coalescing.	*E. cingens*
	Filaments not coalescing.	3
3.	In other algae.	*E. viridis*
	In aquatic phanerogams.	*E. russelliae*

(1) *Entocladia viridis* Reinke

Newton, *Handb. Brit. Seaw.* p. 62, 1931; Collins, Green Alg. N. Amer. p. 279, 1909 (as *Endoderma viride*).

Filaments usually much branched, 3–8μ (average 6μ) dia., 1–6 times as long as broad, cylindrical, more often irregularly contorted and swollen; plastid covering the wall, containing one pyrenoid; terminal cell blunt or tapering. (Fig. 87.)

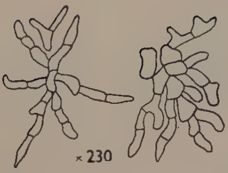


Fig. 87. *Entocladia viridis.* (After Printz.)

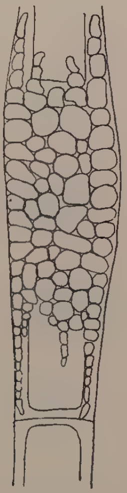


Fig. 88. *Entocladia cingens.* (After Setchell & Gardner.) (× 125.)

Distribution. Local: In *Hormosira* (Bay of Islands). General: Europe, Bermuda, N. America.

This species in the northern hemisphere has a southern range and it is therefore likely to be restricted to the North Island in New Zealand.

(2) *Entocladia cingens* Setch. & Gardn.

Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 291, pl. 18, fig. 7, 1920.

Thallus early forming a pseudo-parenchymatous tissue surrounding the filaments of the host, having a few marginal filaments extending parallel with the long diameter of the host; cells in the centre of the thallus nearly iso-diametric, 5–8μ dia., enlarging to form sporangia; cells of free marginal filaments 3–4μ dia., 2–3 times as long as broad, terminal cells long, conical. (Fig. 88.)

Distribution. Local: on the older joints of *Chaetomorpha aurea* wherever the host occurs. General: S. California.

In the type habitat the species also frequents a *Chaetomorpha, C. californica.*

(3) **Entocladia russelliae** sp.nov.

Filamentis parum ramosis, e sat paucis cellulis constantibus, 5–7μ dia., 1–4-cies longioribus quam latioribus, cellulis cylindricis vel irregulariter tumescentibus et contortis; cellula terminali paulatim descrescente.

Filaments not much branched, consisting of only a relatively small number of cells, 5–7μ dia., 1–4 times as long as broad, cells cylindrical, or irregularly swollen and contorted; terminal cell tapering. (Fig. 89.) Type specimen from Russell in Herb. Auck. Inst.

DISTRIBUTION. Local: in dead phanerogamic material, mangrove swamp (Russell). Endemic.

Russell and the Bay of Islands have proved such a prolific hunting ground that this species is named to commemorate the fact.

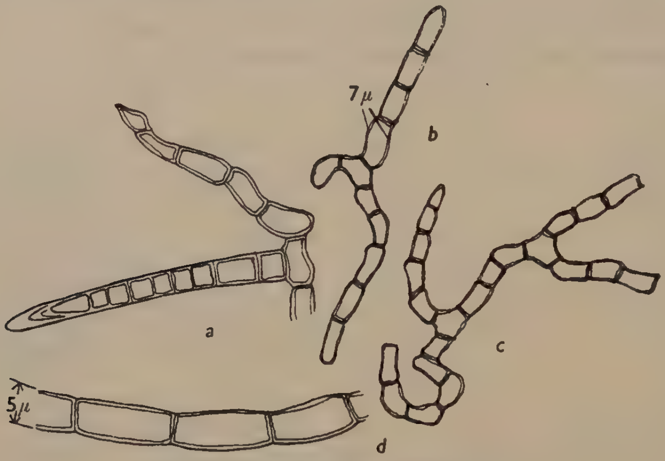


Fig. 89. *Entocladia russelliae.*

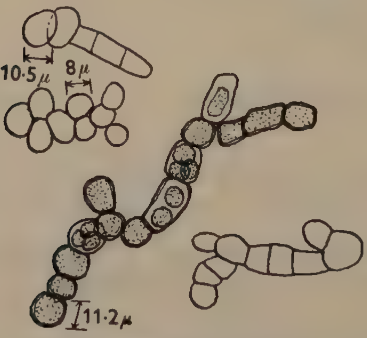


Fig. 90. *Entocladia rivulariae.*

(4) **Entocladia rivulariae** sp.nov.

Thallo e filamentis cellularum brevibus constante, simplici vel ramoso, soluto vel in materiam solidam coeunte; cellulis 9–11μ dia.; chloroplastio viridi, cellulam complente; generatione per zoogonidiis, 2–3 in cellulis singulis, facta.

Thallus consisting of short threads of cells, simple or branched, independent or fusing to form a mass of tissue; cells 9–11μ dia., chloroplast green, filling the cell; reproduction by swarmers, 2–3 per cell. (Fig. 90.) Type specimen in Herb. Auckland Inst.

Distribution. Local: in *Rivularia vieillardii*, Bay of Islands. Endemic.

This differs from *E. cyclostoma* (Waern, 1952) which is unbranched and occurs in *R. biasolletiana*.

Pilinia Kütz.

Basal layer of abundantly branched filaments, from which arise erect filaments, simple or branched, sometimes terminating in multicellular hairs; chloroplast covering entire cell wall; sporangia roundish, ovoid or clavate, terminal or lateral on erect filaments; zoospores biciliate.

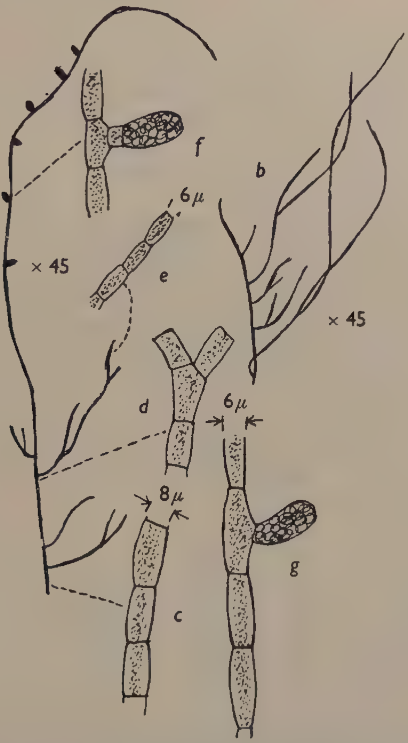


Fig. 91. *Pilinia rimosa*: *a*, *b*, plants; *c–f*, parts of plant, enlarged; *g*, sporangium.

Pilinia rimosa Kütz.

Newton, *Handb. Brit. Seaw.* p. 60, fig. 46, 1931; Kützing, *Tab. Phyc.* 4, pl. 90, 1854.

Thallus with a prostrate system of somewhat irregular cells, more or less torulose; erect filaments up to 2 mm. long, simple or branched irregularly, cells cylindrical or torulose, 6–10μ dia., 1–2 times as long as broad; sporangia ovoid, 12–20μ long, average 16μ, 6–12μ wide, average 8μ, sessile or on a one-celled stalk, usually lateral on the longer erect filaments, more rarely terminal on short branches; forming a dense yellowish green stratum on woodwork. (Fig. 91.)

Distribution. Local: Russell (on woodwork). General: Europe, New England, and probably elsewhere.

The diameter of the filaments is slightly smaller than that given by Collins (1909) and they are longer than those depicted by Newton. Newton's figure also shows hairs which are not mentioned by Collins. It is possible that more than one species is involved here. The material agreed with Collin's description in that it forms a very compact coating that can be removed in pieces of considerable size.

Gomontia Born. et Flah.

Plants perforating shells or wood, described as consisting of creeping, branched filaments, cells irregular, often crowded; chloroplast lobed or reticulate, cells with 1–6 nuclei; sporangia much enlarged with thick walls and special projections from the surface.

There is some evidence that the filamentous stages may belong to other plants, in which case the reproductive portion could be referred to the Chlorococcaceae as suggested by Kylin (1935). For the present the species is placed here.

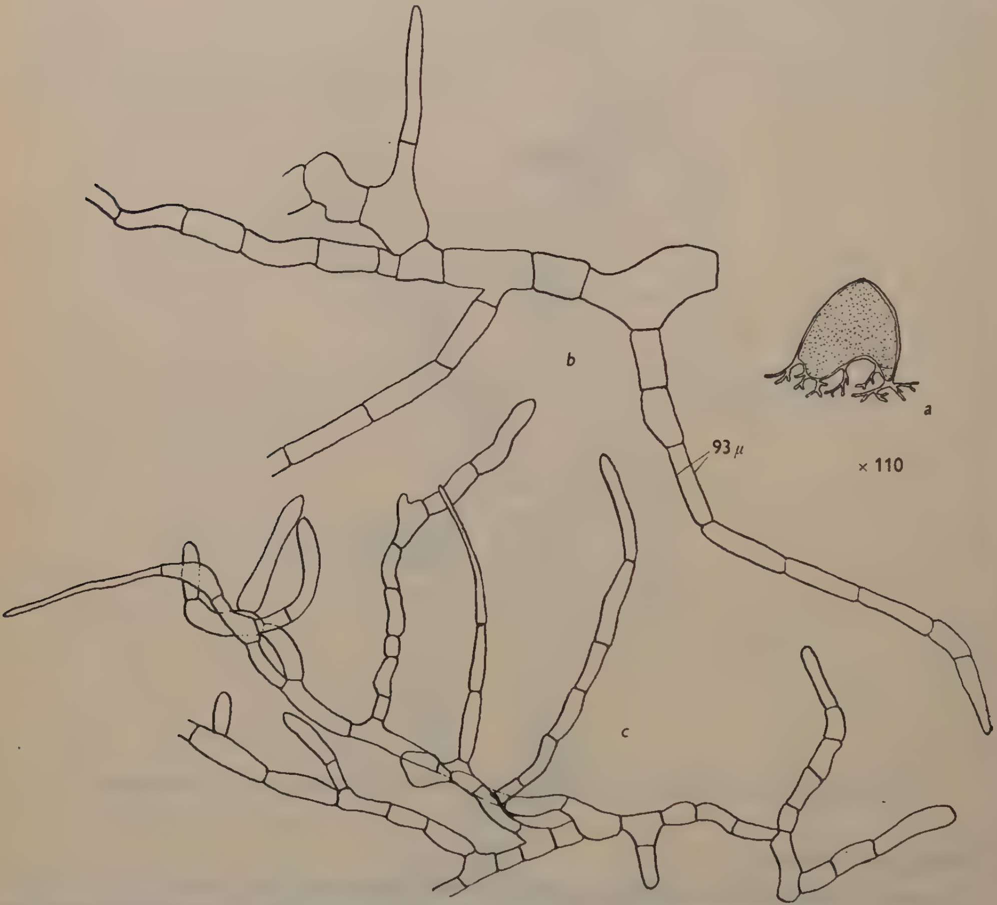


Fig. 92. *Gomontia polyrhiza*: *a*, sporangium; *b*, *c*, *Cladophorella marina*. (*a*, after Setchell & Gardner.)

Gomontia polyrhiza (Lagerh.) Born. & Flah.

Taylor, *Mar. Alg. N.E. North Amer.* p. 58, 1937; Newton, *Handb. Brit. Seaw.* p. 96, 1931; Kylin, *Fysiogr. Sällsk. Förhandl.* **5**, p. 3, 1935; Laing, *Trans. N.Z. Inst.* **57**, 134, 1926; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 90, 1923.

Plant colouring the shell grass green, filaments widely and irregularly branched, 4–8μ dia., sporangia 30–125μ dia., 150–250μ long. (Fig. 92.)

Distribution. Local: Bay of Islands, Auckland, Port Chalmers, probably widely spread. General: North Carolina to New Brunswick, Europe.

SIPHONOCLADALES

Thallus usually of abundantly branched filaments or of scarcely branched vesicular sacs, septate, divisions multinucleate; chloroplasts single and reticulate or numerous and discoid; reproduction by asexual spores or isogametes.

1.	Mature thallus forming a net.	Microdictyaceae
	Mature thallus otherwise.	2
2.	Filaments simple or branched, septate from start.	3
	Filaments branched, septation delayed.	Valoniaceae
3.	Short threads forming a mucilaginous stratum.	Wittrockiellaceae
	Threads long, not forming a mucilaginous stratum.	Cladophoraceae

I have followed Fritsch (1935) in placing the Wittrockiellaceae in the same assemblage as the Cladophoraceae rather than West (1916), who placed it with the Chaetophoraceae.

MICRODICTYACEAE

Microdictyon Dcne.

Plant a sessile, membranaceous network, formed of monosiphonous filaments, densely branching in one plane in a radiate manner, the tips of the branches attaching themselves to the sides of other branches by a terminal thickening, producing irregular, angular, open spaces between the segments; segments multinucleate; chloroplasts reticulate; basal attachment by rhizoidal filaments; reproduction by zoospores formed in any segment.

1.	Primary segments 100–160μ dia., walls thin, habit spongiose.	*M. mutabile*
	Primary segments 150–200μ dia., walls thick, habit not spongiose.	*M. umbilicatum*

Microdictyon mutabile Dellow

Dellow, *Rec. Auck. Inst. Mus.* 4 (1), 3, 1950.

Thallus bright green when fresh, dull blackish green when dried, cushion-like, or rosulate fronds irregularly lobed; branching distichous to irregular, often in more than one plane at periphery, flabellate or rectangular; venation not conspicuous; 3–5 primary radiating filaments; angle of branching usually acute, becoming wider towards periphery of frond; attachment by narrow, thin-walled, often elongated rhizoidal cells; septa present or lacking; rhizoidal cells 300–1400μ long, simple or irregularly forked, growing either from base of main filaments or downwards from a joint which lies more or less parallel with and close to substratum; secondary segments anastomosing or free; anastomosis by annular rings at tips or occasionally along adjacent walls of segments; mesh when present usually triangular, 0·2–0·5 mm. in longest diameter; primary segments 300–600μ long, 100–160μ broad, slightly swollen at upper ends; cells in general becoming smaller towards margins of fronds; secondary anastomosing segments 190–360μ long, 50–90μ wide, smaller in diameter at distal end; apices of terminal segments obtuse; walls thin, lateral walls 1–2μ thick, terminal walls 3–6·5μ; reproductive cells distinguished by conical projections near apex of each cell, unilaterally arranged. (Figs. 93, 93 A.) V.W.L. 307 as *M. umbilicatum*.

DISTRIBUTION. Local: Long Bay, Otehei Bay, Leigh, Stanmore, Orewa, Whangaparaoa Hds, Hen and Chickens Is., Arkles Bay, Narrow Neck, Howick, St Heliers, Rangitoto, Noises, Mayor Is., Great Barrier Is., Motutapu. Endemic.

In the past this plant has formerly been regarded as the same as the Australian *M. umbilicatum*, but Dellow (1950) has shown that the two plants are quite distinct. The New Zealand plant is especially characterized by its spongiose habit.

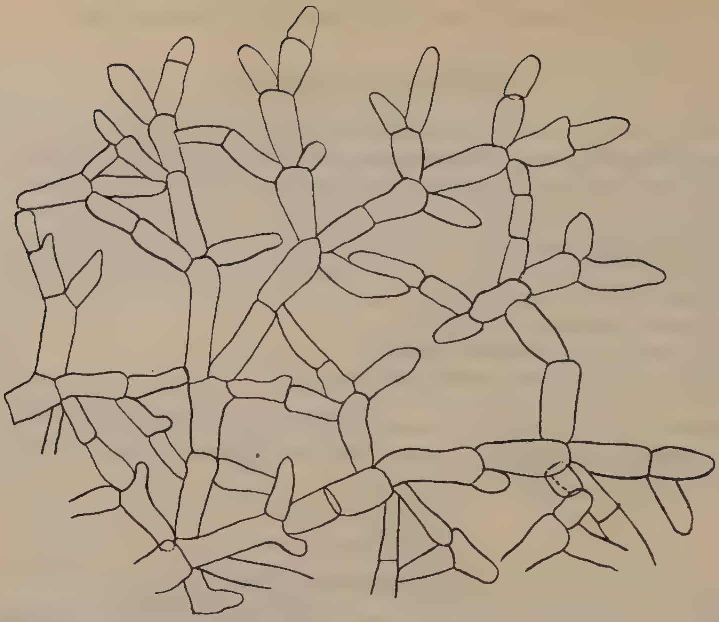


Fig. 93. *Microdictyon mutabile*: portion of the outer part of a fan (×30). (U. V. Dellow.)

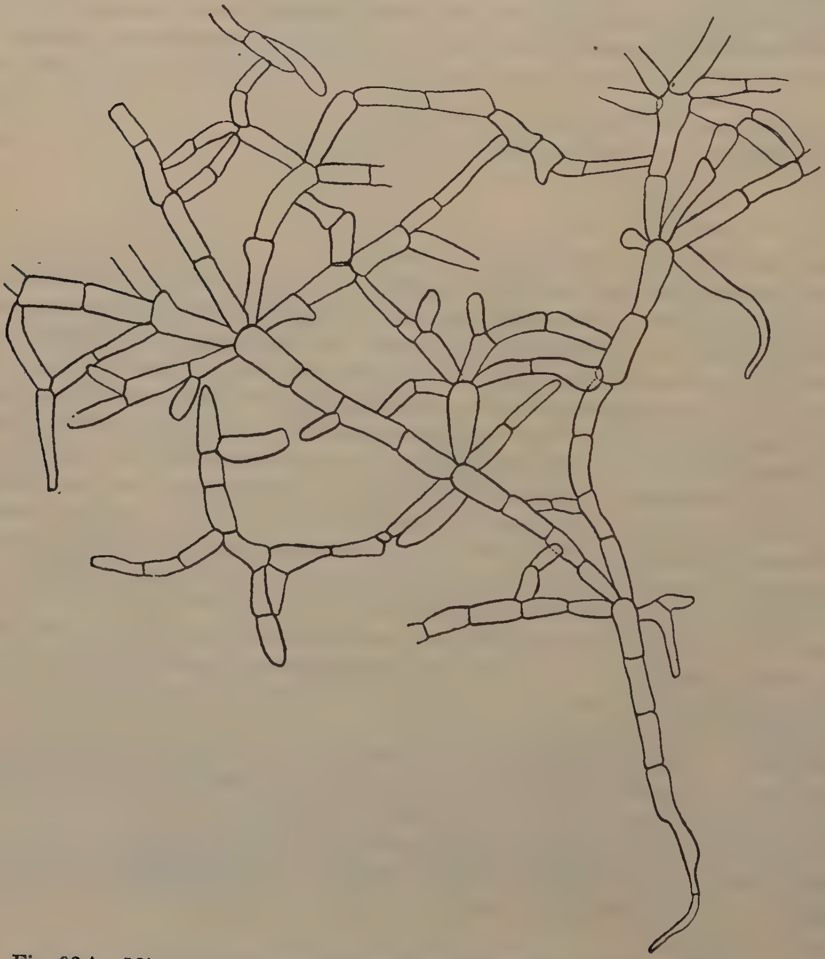


Fig. 93 A. *Microdictyon mutabile*: basal part of a fan (×17). (U. V. Dellow.)

(2) *Microdictyon umbilicatum* (Velley) Zanard.

Setchell, *Univ. Calif. Publ. Bot.* **14**, 503, 1929.

Frond ample, dark green, rigid, up to 6 cm. (–30 cm.) dia., lobed or lacerate; primary filaments 150–200μ dia., $1\frac{1}{2}$–3 times as long as broad, walls 6–8μ or more thick, stratified; secondary filaments 120–140μ dia., ultimate segments 40–55μ, tapering gradually to blunt tip; branching alternate or opposite but in primary filaments in fours or fives from the same point. (Fig. 94.)

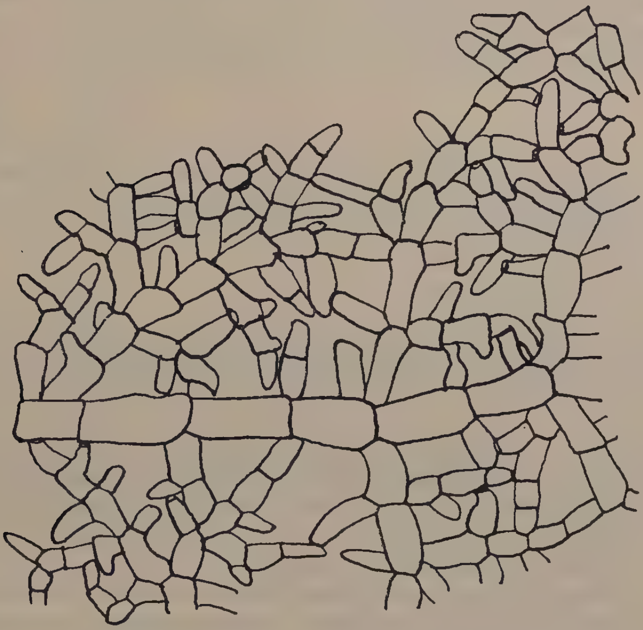


Fig. 94. *Microdictyon umbilicatum.* Cell shape and branching at periphery of thallus (× 53). (After Setchell.)

Distribution. Local: Mayor Is. General: Australia, Friendly Is.

The plants from Mayor Island had well-developed fronds and lacked the typical spongiose habit of *M. mutabile.* The fronds were not as big as material I have seen from Australia. Miss Dellow has examined this collection and considers it to be this species rather than *M. mutabile.* In view of the occurrence of *M. umbilicatum* in Australian and South Pacific waters one would expect it to occur in New Zealand.

Cladophoraceae

Fronds of simple or branching monosiphonous filaments, free or more or less united laterally; septa frequent, enclosing segments with few to many nuclei; chloroplasts broad, reticulate or polygonal, lenticular, but arranged in a network and at times connected by slender strands; multiplication by fragmentation and by akinetes; reproduction by 4-ciliated (or possibly 2-ciliated) zoospores and by 2-ciliated isogametes, formed in segments slightly, if at all, differentiated.

1.	Filaments simple, unbranched.	2
	Filaments branched or with rhizoidal branches.	5
2.	Filaments soft, flaccid, gelatinous, cells broader than long.	*Hormiscia penicilliformis*
	Filaments soft or rigid, cells as long as or longer than broad.	3

3. Filaments with few nuclei per cell. *Rhizoclonium*
   Filaments with many nuclei per cell. 4
4. Filaments more than 100μ dia., usually sessile, attached by an elongated basal cell. *Chaetomorpha*
   Filaments usually less than 100μ dia., free living *Lola*
5. Filaments branched. 6
   Filaments simple or branched but with rhizoidal outgrowths. 7
6. Major portion of plant body composed of long aerial branched threads. *Cladophora*
   Plant body of prostrate, horizontal branched, short threads. *Cladophorella marina*
7. Filaments simple, with rhizoidal outgrowths. *Rhizoclonium*
   Filaments branched at base and with rhizoidal outgrowths. *Rama*

Cladophorella Fritsch

Plant body a complex system of large-celled, horizontal threads attached to substrate by unbranched, usually non-septate, rhizoids; cells possessing a cuticle; reproduction by fragmentation and akinetes.

(1) **Cladophorella marina** sp.nov.

Thallo constante ex axe primario serpente ad solum per rhizoides adhaerente et praedito filamentis erectis aeriis sparse dichotome ramosis, cellulis apicalibus dense completis; omnibus parietibus crassis lamellatis; chloroplastio reticulato; generatione vegetativa per fragmentationem facta.

Thallus consisting of a creeping main axis attached to the ground by rhizoids and with erect aerial filaments sparsely dichotomously branched with dense contents in the apical cells; cell walls thick, lamellated, chloroplast reticulate; vegetative reproduction by fragmentation. (Fig. 92, *b*, *c*.) Type specimen from Orongo Bay in Herb. Auckland Inst.

DISTRIBUTION. Local: Orongo Bay, Uruiti Bay.

So far as can be seen this plant agrees closely with the general characters of the genus *Cladophorella* as recorded by Fritsch (1935). No other method of reproduction other than by fragmentation has been observed.

Cladophora Kütz.

Plants composed of filaments of a single series of segments, filaments branching, usually abundantly; branching lateral, often apparently dichotomous as original filament displaced laterally by a branch; growth primarily apical; branches all of same type, but those of different orders usually differing in size; segments multinucleate, chloroplast reticulate or consisting of numerous small disks; pyrenoids several in a segment; reproduction by 4-ciliate zoospores or biciliate gametes.

The genus is notoriously difficult and I am most grateful to Dr H. K. Phinney who has determined much material that was sent to him. The key and descriptions are the work of the writer. The genus is usually subdivided into *Eucladophora*, *Spongomorpha* (*Acrosiphonia*) and *Aegagropila* and this procedure has been followed. With two exceptions all the species belong to the *Eucladophorae*.

Key to species in local flora

1. Thallus with interwoven rhizoidal branches. 2
   Thallus without interwoven rhizoidal branches. 3
2. Apices of ultimate branches obtuse. *Spongomorpha arcta*
   Apices of ultimate branches distinctly acute. *Acrosiphonia pacifica*
3. Main axis usually more than 150μ. 4
   Main axis usually less than 150μ. 10

4.	Cells of main axis more than 8 times longer than broad.	5
	Cells of main axis less than 8 times longer than broad.	8
5.	Cells of main axis 160–200μ dia., 15–17 times as long as broad.	*C. colensoi*
	Cells of main axis more than 200μ dia.	6
6.	Cells of main axis 8–13 times longer than broad, with numerous down-growing unicellular rhizoids, brownish green.	*C. prolifera*
	Cells of main axis 12–40 times longer than broad, down-growing rhizoids few, grass green.	7
7.	Cells of main axis 12–20 times longer than broad, upper cells 2 times as long as broad.	*C. radiosa*
	Cells of main axis 20–40 times longer than broad, upper cells 5–6 times as long as broad.	*C. feredayi*
8.	Cells of main axis 6–8 times longer than broad.	9
	Cells of main axis 2–5 times longer than broad.	*C. fascicularis*
9.	Cells of main axis 100–250μ.	*C. utriculosa*
	Cells of main axis 330–350μ.	*C. valonioides*
10.	Main axis less than 35μ dia.	*C. aucklandica*
	Main axis more than 35μ dia.	11
11.	Branching more or less restricted to base, branches elongate, dilating to apex.	*C. verticillata*
	Branching all over or more or less restricted to apex, branches not dilating above.	12
12.	Cells of main axis 35–80μ.	13
	Cells of main axis 80–150μ.	20
13.	Cells of main axis 1–3 times longer than broad.	14
	Cells of main axis more than 3 times longer than broad.	15
14.	Main axis 40–50μ, cells 1½–2 times as long as broad.	*C. daviesii*
	Main axis 70–75μ, cells 2–3½ times as long as broad.	*C. crinalis* var. *eramosa*
15.	Plant always free floating, cells 4–20 times longer than broad.	*C. crispata*
	Plant usually attached, cells 3–6 times longer than broad.	16
16.	Plants not more than 5 cm. long.	19
	Plants more than 5 cm. long.	17
17.	Dark green, ends of major branches naked, elongate.	*C. polyacantha*
	Grass green, ends of major branches not naked.	18
18.	Cells of main axis 37–45μ, branchlets few, spiny, irregular.	*C. simpliuscula*
	Cells of main axis 45–60μ, numerous alternate or secund branchlets.	*C. glaucescens*
19.	Ramuli and branchlets patent, acute.	*C. crinalis*
	Ramuli and branchlets recurved, blunt.	*C. albida* var. *refracta*
20.	Fronds floating except in earliest stages.	21
	Fronds always attached.	22
21.	Cells of main axis 40–100μ, cells 4–8 times longer than broad.	*C. gracilis* var. *vadorum*
	Cells of main axis 100–150μ, cells 3–5 times longer than broad.	*C. expansa*
22.	Thallus forming a low pulvinate mass.	26
	Thallus erect.	23
23.	Upper branches and ramuli reflexed.	*C. refracta*
	Upper branches and ramuli erect.	24
24.	Branchlets 140–150μ, same diameter as axis.	*C. laetevirens* var. *regularis*
	Branchlets narrower than axis.	25
25.	Plants whitish to pale green, vitreous.	*C. ceratina*
	Plants pale or glaucous green.	*C. gracilis*
26.	Lower cells 2–5 times longer than broad.	*C. frascatii*
	Lower cells 6–8 times longer than broad.	*C. repens* f. *tenuis*

(1) *Acrosiphonia pacifica* Kütz.

Kütz., *Sp. Alg.* p. 419, 1849; Mont., *Voy. Pole Sud. Bot.* 1, 7, pl. 14, fig. 2, 1842–45; Laing, *Trans. N.Z. Inst.* 57, 133, 1926 (as *Cladophora pacifica*); Hooker *Fl. Ant.* 1, p. 192 (as *C. pacifica*) 1847; Hooker, *Handb. N.Z. Flora*, p. 717, 1867 (as *C. pacifica*).

Plant when young forming a compact cushion, confluent, spongy, composed of capillary filaments, rigid, much branched and densely imbricate; older plants with caespitose tufts arising from basal area; branches simple below, dichotomously or alternately branched above, beset with subsecund branchlets, erect or uncinate with acute terminal cells; cells of branches 56–123μ dia., usually 90–100μ, as long as broad to 3 times as long as broad; colour dark olive green. (Fig. 95, Pl. 35.)

Distribution. Local: Auckland Is., Stewart Is. (Pegasus), Campbell Is., Chatham Is.

The colour is dull green to olive and the cushions are 2·5–10 cm. high. The very characteristic appearance of this plant is unmistakable, and also there are the acute apices of the branchlets which clearly demarcate it from *Spongomorpha arcta*.

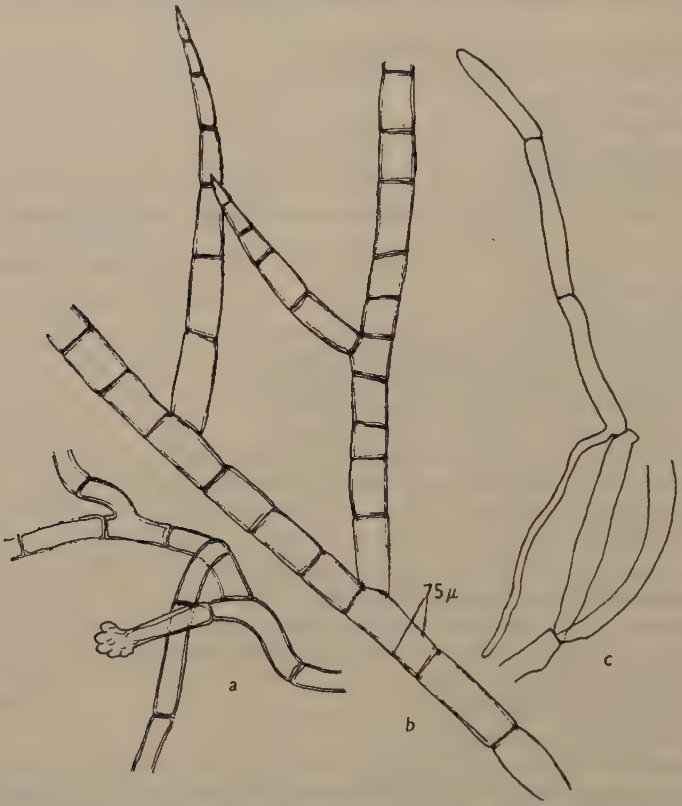


Fig. 95. *Acrosiphonia pacifica*: *a–c*, rhizoidal branches; *b*, ultimate aerial branches.

(2) *Spongomorpha arcta* (Dillw.) Kütz.

Kütz., *Phyc. Gen.* p. 263, 1843; Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 223, 1920.

Plants rich green in dense fastigiate tufts, up to 15 cm. high; young plants pulvinate, becoming more matted, tufted and compact with age; filaments erect, stiff, 60–100μ dia. above, smaller below, much branched; branches erect or appressed, obtuse or clavate at tips; cells above 4–6 times longer than broad, lower cells 1·5–3 times; rhizoidal descending branches 40–60μ dia., cells 2–6 times as long as broad, firmly matting together the lower part of the tuft. (Fig. 95 A.)

Distribution. Local: Stewart Is., Auckland Is., Campbell Is. General: Europe, N.E. North America, Alaska to Washington.

This species is widely distributed in cold waters of the northern hemisphere. Its occurrence in the southern hemisphere provides an apparent example of discontinuity. It is likely that the species may also occur in South America and in the Antarctic Islands, thus indicating a course of migration comparable to that of *Macrocystis*.

The young plants form more or less hemispherical tufts, then as they mature erect filaments grow out and form compact fascicles which later become sea worn and almost smooth. The habit of the plant may therefore vary considerably.

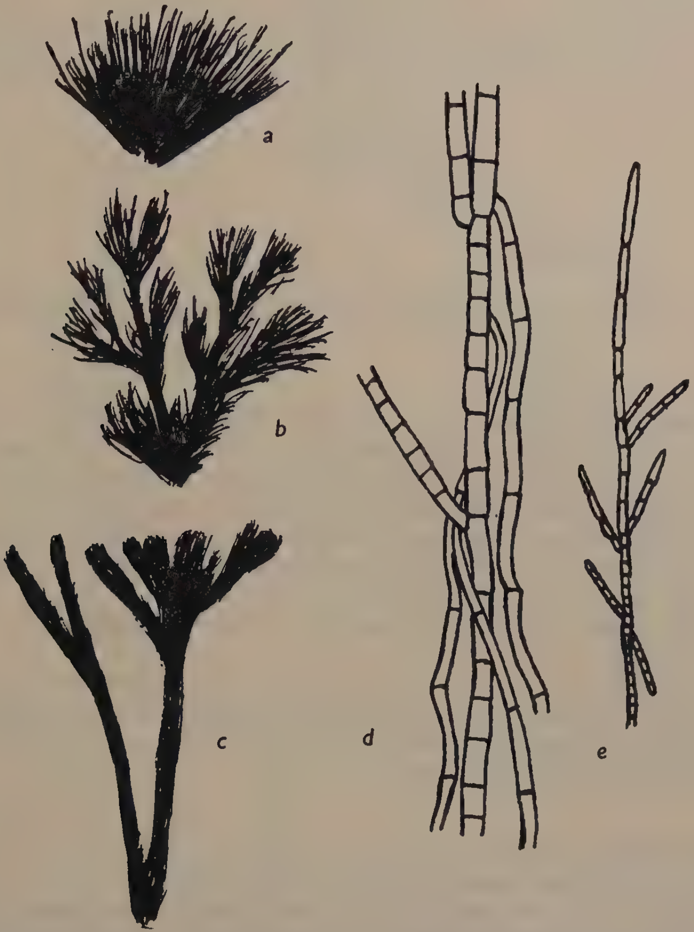


Fig. 95 A. *Spongomorpha arcta*: *a*, youngest growth stage; *b*, intermediate; *c*, oldest growth stage; *d*, portion of plant with down-growing filaments (× 37); *e*, terminal portion (× 8). (*a–b*, × 1.) (*d*, *e*, after Hamel.)

(3) *Cladophora valonioides* Sond.

Sond., Alg. Trop. Austral. p. 1, 1871; Kütz., *Sp. Alg.* p. 391, 1849.

Plants up to 2 cm. tall or more, composed of rigid filaments, much branched, branching dichotomous, main axis at base 330–350μ wide, wall 20–23μ thick, distinctly lamellated; branches arranged in twos or threes or verticillate; articulations cylindrical, lower cells 6–8 times, upper 3–5 times, longer than broad; apices obtuse; plant light green, adheres imperfectly to paper. (Fig. 96.)

Distribution. Local: Cape Maria, 90 Mile Beach, Hen and Chicken Is., Russell, Fifeshire Rock, Piha, Orewa, The Mount, Waihau Bay, Castle Point, Makara, St Clair. General: Tasmania, South Australia.

This species is easy to recognize because it forms moss-like tufts, very compact, and the filaments are coarse with the distinctive dichotomous branching, very readily visible towards the base. Reinbold (1899) transferred this species to *Siphonocladus*, but it is not clear on what grounds he made this decision and it seems better left as a *Cladophora*.

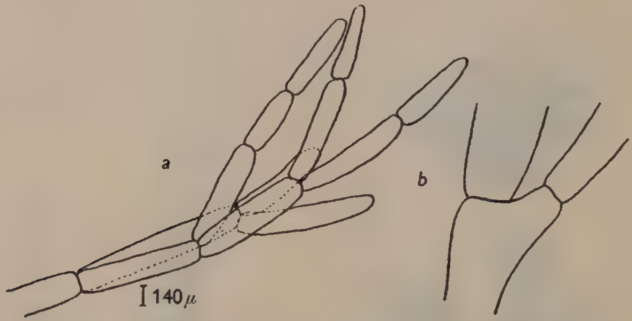


Fig. 96. *Cladophora valonioides*: *a*, part of the apical portion of thallus; *b*, branching.

(4) *Cladophora colensoi* Harv.

Harv., in Hooker *Fl. Nov. Zel.* **2**, p. 262, 1855; Hooker, *Handb. N.Z. Flora*, p. 718, 1867; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877.

Filaments up to 22 cm. high, caespitose, dark green, rigid, flexuose, primary branching mainly from the base; branches elongate, curved, bare at the base, beset with ramuli at the apices, ramuli often secund, appressed, short or long; cells of main branches 160–200μ, 15–17 times longer than broad, walls thick, lamellate; cells of ramuli 75–150μ, 1½–4 times as long as broad, walls thick. (Pl. 36.) V.W.L. 304.

Distribution. Local: Russell, St Heliers, Fletcher's Bay, Hawke's Bay, the Kaik, Stewart Is. Endemic.

The filaments are narrower than those of *C. verticillata* and the cells of the main axis tend to be shorter. The main difference is in habit, this species being much more flexuous, and the branches bear numerous ramuli which do not dilate towards the apices. It differs from *C. radiosa* in the dark green colour.

(5) *Cladophora radiosa* (Suhr.) Kütz.

Suhr., *Flora*, p. 741, 1840; Kütz., *Sp. Alg.* p. 422, 1849.

Plant stipitate, rigid, 5–18 cm. tall; filaments flexuose, grass green, drying to a vitreous green, much branched, fastigiate; branches flexuous, beset with numerous ramuli, branching typically opposite; lower cells 12–20 times longer than broad, upper cells 2 times as long as broad, inflated. (Fig. 97.)

Distribution. Local: Russell, Timaru. General: Algoa Bay.

In habit this plant is very like *C. feredayi* from which it differs in the cell measurements. It may be suggested that perhaps the species is only a variety of *C. feredayi*.

(6) *Cladophora feredayi* Harv.

Harv., *Phyc. Aust.*, tab. 47, 1858–63; J. Ag., De Alg. Nov. Zel. Mar. p. 3, 1877 (as *C. pellucida*); Laing, *Trans. N.Z. Inst.* **57**, 134, 1926 (as *C. pellucida*).

Plants up to 18 cm. long, stipitate, light green, drying a glassy green, rigid; filaments long, setaceous, angularly flexuose, di- to trichotomously or alternately branched; branches discrete or interwoven, flexuose, much divided; ultimate ramuli densely fasciculate; articulations of branches long, cylindrical, 20–40 times longer than broad, in branchlets constricted at the joints, 5–6 times longer than broad. (Pl. 37.) V.W.L. 202, as *C. pellucida*.

Distribution. Local: Bay of Islands, Auckland, Pihama, Timaru, Kaikoura, Shag Pt, Warrington, Green Is., St Clair, Brighton, Colne Bay, Bluff, Stewart Is., Chatham Is. and probably elsewhere. General: Tasmania, Australia, New Zealand.

There is some degree of variation in the habit of this plant which may be associated with the seasons. It is nearly always accompanied by a red parasite in the walls of the basal cell. This is *Schmitziella cladophorae* (Chapman, 1951)[1] and is closely allied to *S. endophloea* which occurs in the allied *C. pellucida* of northern waters. There seems little doubt that the earlier authors were confused by the similarity between this plant and *C. pellucida*.

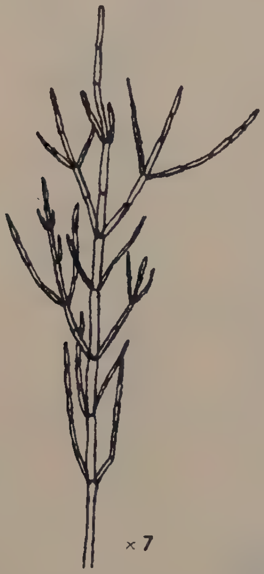


Fig. 97. *Cladophora radiosa*: portion of plant.

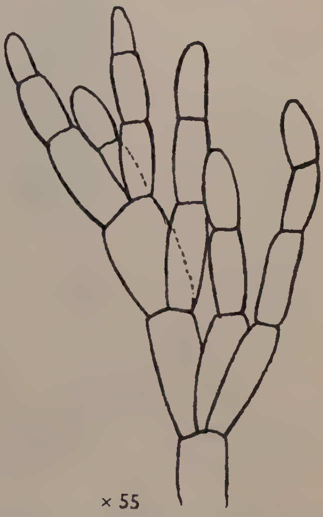


Fig. 98. *Cladophora fascicularis*.

(7) *Cladophora fascicularis* (Mert.) Kütz.

Kütz., *Phyc. Gen.* p. 268, 1843; Collins, Green Alg. N. Amer. p. 265, 1909.

Plants large, 30–50 cm. long; main filaments and principal branches flexuous, sparingly branched, alternate; ends beset with long, pectinate, densely fasciculate ramuli, 1·5–3·0 mm. long; cells of main filaments 200–260μ (–360μ) dia., 2–5 times as long as broad; ramuli 70–120μ dia., 1–3·5 times as long as broad. (Fig. 98.)

Distribution. Local: Bay of Islands on *Hormosira*, Pihama, Otago, Timaru, St Clair. General: North Carolina, Bermuda, Florida, West Indies, Brazil, Peru, Red Sea, South Australia.

(8) *Cladophora utriculosa* Kütz.

Kütz., *Phyc. Gen.* p. 269, 1843; *Tab. Phyc.* **3**, tab. 94, 1853.

Tufted, light or dull green, 10–20 cm. long; filaments firm, submembranaceous, di-polychotomous, 100–250μ dia. near base, 70–100μ in the upper parts, which are set with lateral, often secund, ramuli; cells 6–8 times as long as broad below, 2–4 times above. (Fig. 99.)

Distribution. Local: Auckland, Tauranga, Charteris Bay, Nelson, Otumoetai Beach, Kena Beach, Portobello, Otago Harbour, Wycliffe Bay, Akaroa, Lyall Bay, Lyttelton, Bluff (Southland), Dusky Sd, Pegasus. General: North Atlantic east and west, Mediterranean, Brazil.

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[1] Notes on New Zealand Algae. *Trans. Roy. Soc. N.Z.* **79** (1), 84.

It has been suggested that *C. daviesii* is not a good species and should be included in *C. utriculosa* or *C. fascicularis*. The diagnosis of *C. daviesii* states that the cells are regularly 2 times as long as broad and I consider that plants agreeing with this do occur in New Zealand.

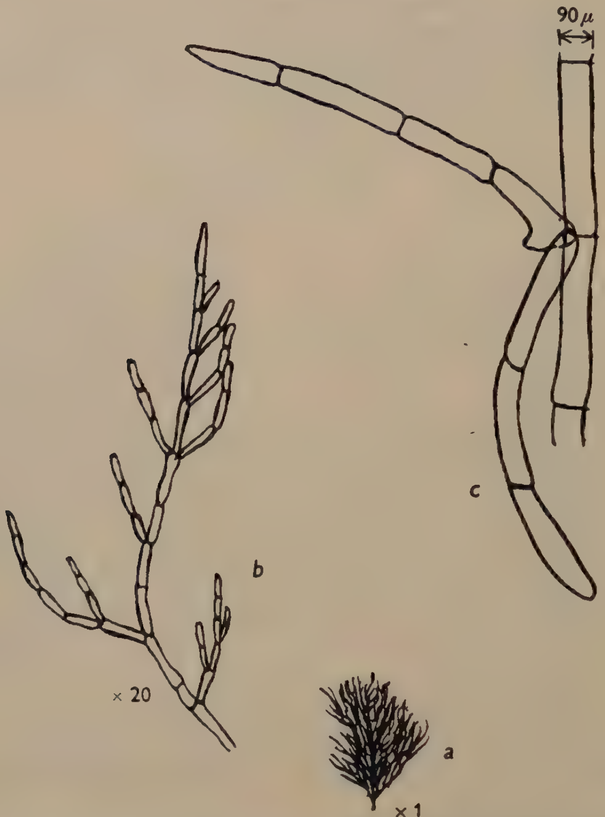

Fig. 99. *Cladophora utriculosa*: *a*, small plant; *b*, *c*, branching.

(9) *Cladophora aucklandica* Rabenh.

Rabenh., *Hedwigia*, **17**, p. 65, 1878; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926.

Plant dull green, 18–20 cm. or more long, sparsely branched; filaments 32μ dia. at base; branches not greatly rebranched, cells of branches 10–15μ dia., 6–10 times longer than broad, more or less constricted at the septa; cell wall thick, hyaline, more or less striate; chloroplast granular.

DISTRIBUTION. Local: Auckland Is. General: Auckland Is.

No specimens of this species have been seen by the author. The very narrow main axis renders it extremely distinct. It is possible that this plant is in fact synonymous with *Rama antarctica* or *R. novae-zelandiae* (see p. 465).

(10) *Cladophora verticillata* Hook. & Harv.

Hooker, *Fl. Ant.* **1**, 193, 1844; Laing, *Trans. N.Z. Inst.* **57**, 134, 1926; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877; Hooker, *Handb. N.Z. Flora*, p. 718, 1867.

Plants caespitose, about 10 cm. tall, rigid, setaceous; filaments delicate, strict, hardly divided, branching opposite, ternate or quaternate, lateral branches simple, elongate, bare, erect, fastigiate, slightly dilated towards the apices; articulations of primary branches near base 55–90μ, 6–8 times longer than broad, near apex 120–185μ broad, quadrate or up to 2 times as long as broad. (Fig. 100.)

Distribution. Local: Port William, Auckland Is., Campbell Is., Snares. General: Antarctic Islands of N.Z.

The record for *Cladophora virgata* (Hooker, *Fl. Ant.* **1**, p. 192, 1844; Hooker, *Handb. N.Z. Flora,* p. 718) almost surely refers to *C. verticillata.* The only record given in both works is Auckland Is.

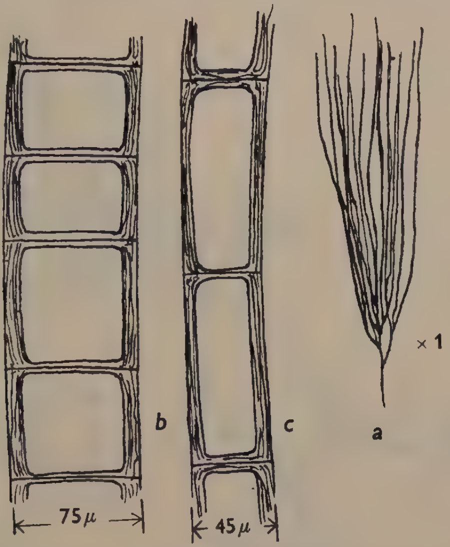

Fig. 100. *Cladophora verticillata*: *a*, plant; *b*, cells of apical portion of branch; *c*, cells at base of branch.

(11) *Cladophora daviesii* Harv.

Harv. in Hooker, *Fl. Nov. Zel.* **2**, 263, 1855; Hooker, *Handb. N.Z. Flora,* p. 718, 1867; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926.

Plant 2·5–12 cm. long, densely caespitose, light green, rigid, profusely branched, main axis and branches 40–50μ dia.; branching alternate or dichotomous, branches bare at base, sometimes reflexed, clothed with ramuli above, secund or corymbose fasciculate, 20–25μ dia.; cells 1½–2 times as long as broad throughout. (Fig. 101.)

Distribution. Local: Tauranga, Titahi Bay, Purakanui. Endemic.

J. Agardh (1877) considered this species was identical with *C. fascicularis,* and Phinney (mscr.) has suggested it is identical with *C. microcladioides.* The plants from New Zealand that I assign to this species do not agree with either and I believe it is a separate entity.

(12) *Cladophora crinalis* Harv.

Harv. in Hooker, *Fl. Nov. Zel.* **2**, 263, 1855; Hooker, *Handb. N.Z. Flora,* p. 718, 1867; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926.

Plants shortly caespitose, 1–5 cm. long, densely interwoven at the base, bright green; filaments thin, rigid, becoming olive or blackish on drying, branches and ramuli erect or adpressed, main axis 48–60μ wide, cells 4–5 times as long as broad; branching dichotomous below, polychotomous above, ramuli frequent or sparse, with more or less acute apices, cells 40μ dia., 1½–3 times as long as broad. (Fig. 102.)

Distribution. Local: Howick, Narrow Neck, Orewa, Leigh, Gannet Rock, Pinnacles, Whangaparapara, Lyall Bay, Purakanui, Blackhead, Port Chalmers, Hoopers Inlet, Green Is., Stewart Is., Island Bay, Tunnel Beach (Dunedin), Portobello, St Clair, Warrington. Endemic.

(13) *Cladophora crinalis* var. **eramosa** var.nov.

Habit as for the parent species, but differing from it in that the main axes are about 70μ wide and the cells 2–3½ times as long as broad. The branching is very sparse and usually only dichotomous. (Fig. 103.) Type specimen in Herb. P.R.B. 69,254 from Stewart Is.

Distribution. Local: St Clair, Warrington, Stewart Is., Riverton, Tunnel Beach. Endemic. The specimens from St Clair and Warrington were recorded by Laing (1926) as *C. simpliuscula*.

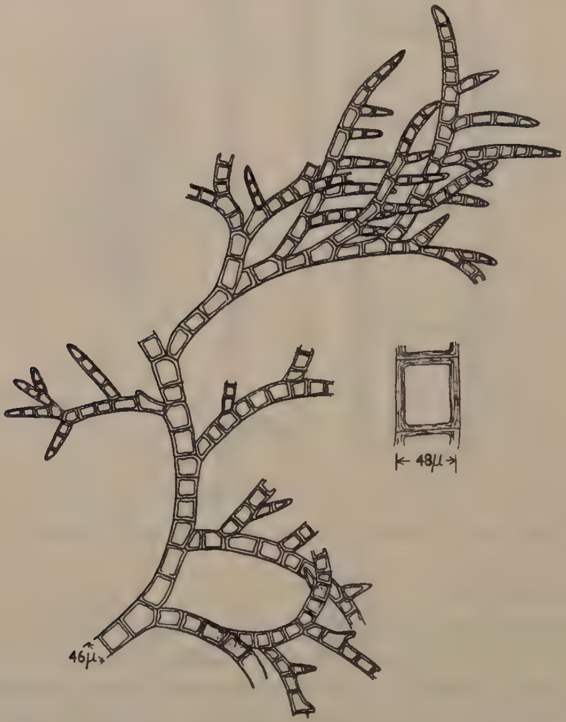

Fig. 101. *Cladophora daviesii*: **portion of plant and single cell from main axis to show wall lamellation.**

(14) *Cladophora crispata* (Roth) Kütz.

Collins, Green Alg. N. Amer. p. 274, 1909.

Forming loose masses floating in the water, main filaments sparingly branched laterally or dichotomously; branching above alternate, more dense, and filaments more slender in each order of branches; main filaments $40–75\mu$, ramuli $20–35\mu$; cells 4–20 times longer than broad, usually longer in ramuli than in axis; ramuli not tapering, obtuse, cell walls thin. (Fig. 104.)

Distribution. Local: Poverty Bay, Lake Grassmere, Ahora Hds, Portobello. General: Fresh and brackish waters of Europe and North America.

(15) *Cladophora polyacantha* Mont.

Collins, Green Alg. N. Amer. p. 257, 1909.

Tufts dull to dark green, 10–20 cm. long, filaments branched dichotomously below, $50–80\mu$ dia., branches long, rather stiff, flexuous, usually with a long naked apex, elsewhere beset with similar long branches, $30–60\mu$ wide, or else with numerous, short, alternately placed, acute, spine-like ramuli $25–40\mu$ dia., composed of 2–3 cells; lower cells of branches 4 times as long as broad, upper cells of branches and ramuli 2–3 times longer than broad. (Fig. 105.)

Distribution. Local: Stewart Is., Waikouaiti. General: Florida, South America.

This species is unmistakable by virtue of the long naked apices and the short 3-celled acute ramuli.

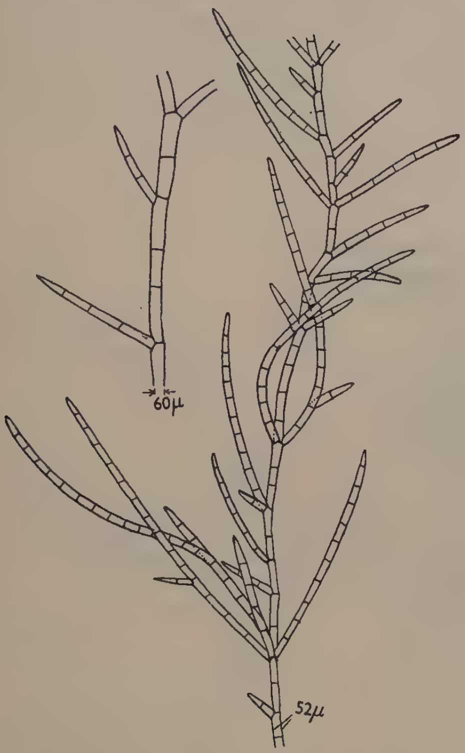

Fig. 102.

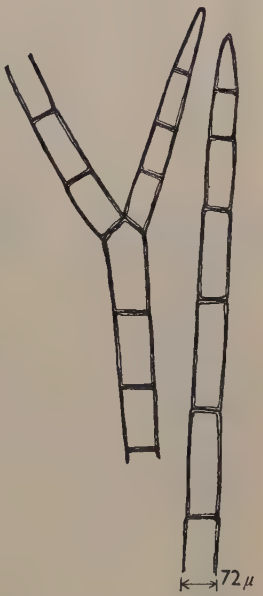

Fig. 103.

Fig. 102. *Cladophora crinalis*: portion of plant and part of plant (left) showing branching near base.
Fig. 103. *Cladophora crinalis* var. eramosa.

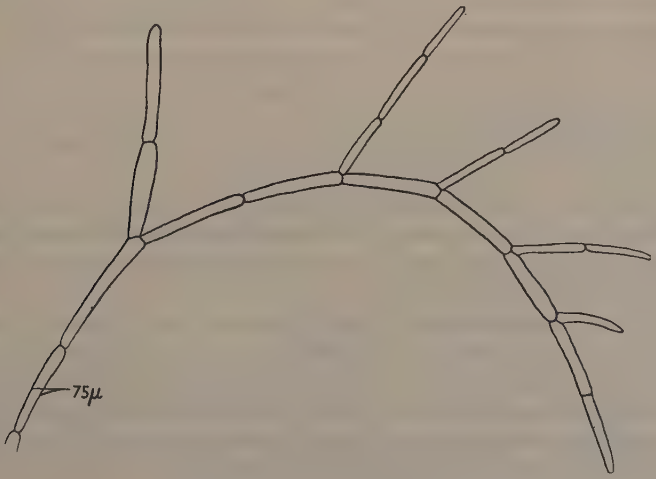

Fig. 104. *Cladophora crispata.*

(16) *Cladophora simpliuscula* Hook. & Harv.

Hooker, *Fl. Ant.* **1**, 193, 1844.

Filaments interwoven, light to dark green, stiff, flexuous, 37–45μ thick, irregularly and sparsely branched; branches very long, simple or with few, short, simple, patent branchlets, rarely secund; cells 3–6 times as long as broad. (Fig. 106.)

Distribution. Local: Stewart Is., Timaru. General: Falkland Is., Cape Horn.

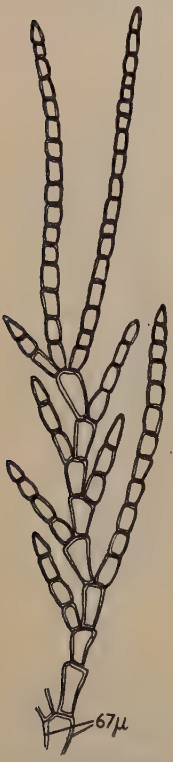

Fig. 105.

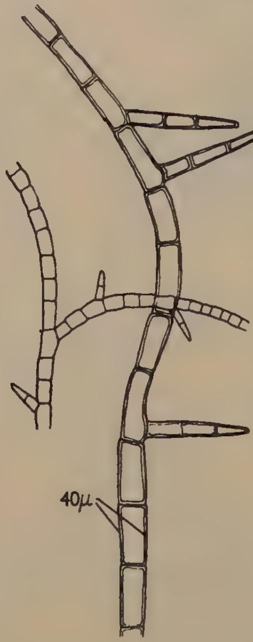

Fig. 106.

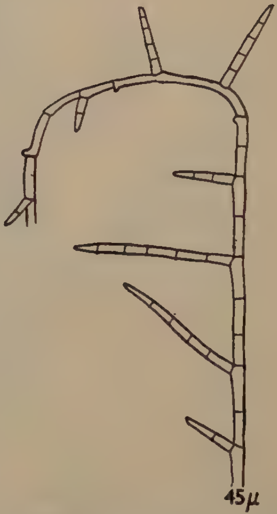

Fig. 107.

Fig. 105. *Cladophora polyacantha.* Part of plant from Stewart Is.

Fig. 106. *Cladophora simpliuscula.* Reproduction of original drawing by Harvey (*Fl. Antarct.*).

Fig. 107. *Cladophora glaucescens*: portion of thallus showing branching.

(17) *Cladophora glaucescens* (Griff.) Harv.

Collins, Green Alg. N. Amer. p. 256, 1909.

Plant 10–40 cm. long, glaucous or yellowish green, loosely tufted, much branched, adhering well to paper, branches ending with numerous alternate or secund ramuli with acute apices; basal cells 45–60μ dia., cells of ramuli 25–30μ, usually 4–6 times as long as broad. (Fig. 107.) V.W.L. No. 327.

Distribution. Local: Lonneker's Nugget (Stewart Is.). General: Atlantic coast of Europe and U.S.A., Vancouver Is. to California.

The specimen distributed by Mr Lindauer agrees very closely with this northern species. An attenuated specimen from Dusky Sound collected by Dr H. H. Allan may belong here, though the branching is not very abundant, in which respect it is more like *C. delicatula*, a species recorded from South Australia.

(18) *Cladophora albida* Kütz. var. *refracta* Thur.

Hamel, *Chlor. Côtes françaises*, II, p. 49, fig. 17*c*, 1930.

Fronds up to 3 cm. long, soft, pale green, much interwoven, spongy, filaments soft, 30–60μ below, cells 2–5 times as long as broad; main branching irregular, branches bearing secund ramuli, patent, obtuse, 16–25μ dia., cells 2–4 times longer than broad, upper branches and ramuli recurved. (Fig. 108.)

Distribution. Local: Pihama, Bluff Hill, Island Bay, Lyttelton. General: France, New Jersey to Maine.

The plant is small and its discontinuous distribution may in part be due to the fact that it has been overlooked elsewhere.

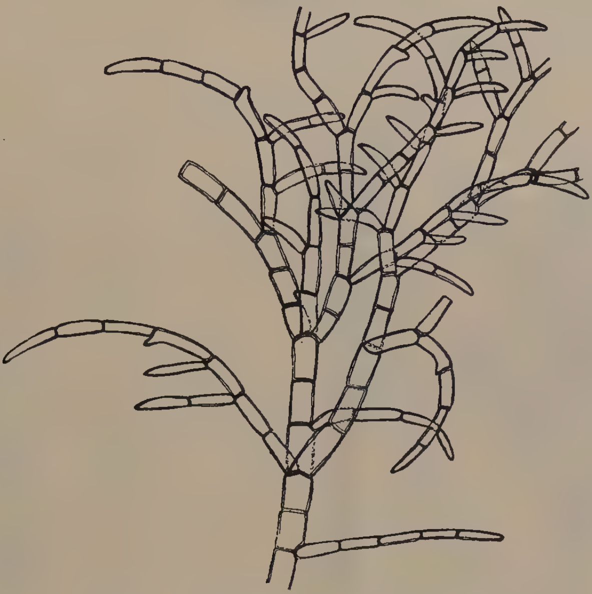

Fig. 108. *Cladophora albida* var. *refracta*.

(19) *Cladophora prolifera* (Roth) Kütz.

Hamel, *Chlor. Côtes françaises*, II, p. 5, 1930.

Plants forming greenish brown tufts up to 10 cm. high, becoming brown on drying; branching di-trichotomous, cells of the main axes 200–300μ, enlarging from the base to the top, 8–16 times longer than broad; cells of the branches 100–250μ, 4–6 times longer than broad; the lower cells of the axis emit numerous uni-cellular, descending rhizoids which may branch at their ends. (Fig. 109.)

Distribution. Local: Kermadec Is. General: Atlantic coast of France, Mediterranean.

Some specimens from the Kermadecs in the Laing Collection agreed very closely with the above description. E. S. Gepp had also seen these plants and labelled them (mscr.) as this species or a variety (possibly because of the discontinuity of distribution). A comparison with material from the Mediterranean indicated that any differences were so slight that they might well be due to the preservation.

I am including here the record of *C. fusca* Mart. (Cotton, *Kew Bull. Misc. Inf.* p. 326, 1912; Laing, *Trans. N.Z. Inst.* 57, 133, 1926) which is also recorded only from the Kermadec Is. I suspect that the plant recorded as *C. fusca* is probably an attenuated form of *C. prolifera*.

(20) *Cladophora gracilis* (Griff.) Kütz.

Kütz., *Tab. Phyc.* **4**, pl. 20, fig. 1, 1854, as *C. vadorum*; Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 216, 1920; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877; Harv. in Hooker, *Fl. Nov. Zel.* **2**, 263, 1855; Hooker, *Handb. N.Z. Flor.* p. 718, 1867.

Plants moderately rigid, forming somewhat slender, pyramidal fascicles, 15–30 cm. high, pale or glaucous green, di- to trichotomous at the base; main axis up to 160μ dia., cells 4–7 times as long as broad; branches smaller and beset with numerous slender, tapering, secund ramuli constricted at the joints. (Fig. 110.)

Distribution. Local: Russell, Parua Bay, Portobello, Otago, Stewart Is., Lyall Bay, Dunedin Wharf, The Kaik, Wycliffe Bay, D'Urville Is., Port William. General: Atlantic coasts of Europe and U.S.A., Alaska, Washington.

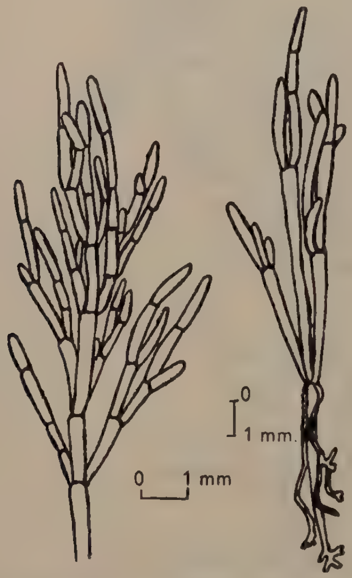

Fig. 109. *Cladophora prolifera.* (After Hamel.)

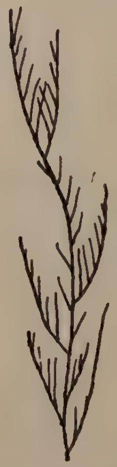

Fig. 110. *Cladophora gracilis* (× 2).

(21) *Cladophora gracilis* var. *vadorum* (Aresch.) Coll.

Collins, Green Alg. N. Amer. p. 263, 1909.

Similar to the parent species but the filaments are more slender, 40–100μ dia., cells 4–8 times as long as broad.

Distribution. Local: Lyttelton (Diamond Harbour). General: Europe, Nova Scotia to New Jersey.

(22) *Cladophora expansa* (Mert.) Kütz.

Hamel, *Chlor. Côtes françaises*, II, p. 40, fig. 14*b*, 1930.

Fronds dull green, loosely branched, main branches 100–150μ dia., cells 3–4 times longer than broad; branches flexuous with smaller, patent, secondary branches, divaricately divided, 82μ dia., cells 4–5 times longer than broad, bearing secund, blunt ramuli, 40–45μ dia., cells 3½–4½ times as long as broad. (Fig. 111.)

Distribution. Local: D'Urville Is. General: Europe, Newfoundland to New Jersey. This species is probably more widespread in our southern waters.

(23) *Cladophora refracta* (Roth) Kütz.

Kütz. *Tab. Phyc.* 4, tab. 10, 1854; Taylor, *Mar. Alg. N.E. N. Amer.* p. 90, pl. 6, fig. 1, 1937.

Plants attached, tufted, dull to greyish green, 10–20 cm. tall, spongy in texture, main filaments rather stiff, 100–120μ dia., much branched, branches close, erect, but upper branches frequently reflexed; branches 20–50μ dia., with obtuse apices; cells 2–3 times as long as broad, wall up to 7μ thick. (Fig. 112.) V.W.L. 277 and 178 (as *Cladophora* sp.).

Distribution. Local: Oeo, Pihama, Kaikoura, Lyall Bay, Moeraki, St Clair. General: Atlantic coasts of Europe and North America.

The regularly reflexed branches are the main feature of this species, but these are not always evident throughout every plant.

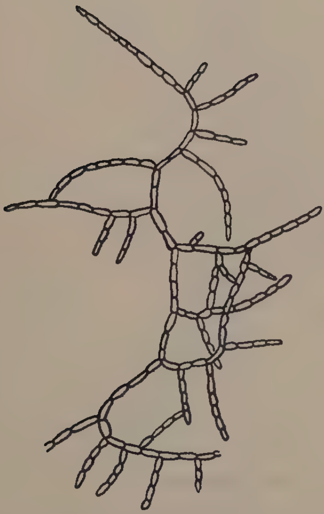

Fig. 111. *Cladophora expansa.* (After Hamel.)

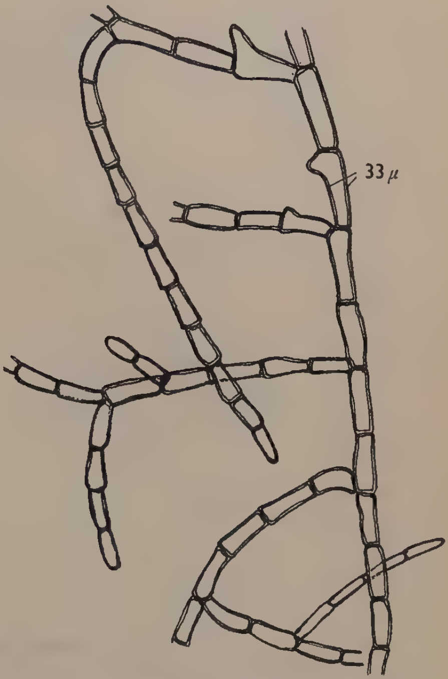

Fig. 112. *Cladophora refracta.*

(24) *Cladophora laetevirens* (Dillw.) Harv. var. **regularis** var.nov.

Planta cristata ad 5 cm. alta; filamentis 140–155μ dia., rigidis, flavo-viridibus, valde ramosis, ramis erectis, saepe oppositis, ramis ultimis brevibus, obtusis vel subacutis, dense fastigiatis ad apices ramorum; cellulis axis primarii 4–5-ies longioribus quam latioribus, ramorum 2½–3-ies longioribus quam latioribus.

Plant tufted, up to 5 cm. tall, filaments 140–150μ dia., rigid, yellow green, much branched, branches erect, often opposite, ultimate ramuli short, obtuse or subacute, densely fastigiate at the tips of the branches; cells of main axis 4–5 times longer than broad, of the branches 2½–3 times longer than broad. (Fig. 113.) Type specimen Herb. P.R.B. no. 44,563, Nelson.

Distribution. Local: drift at Nelson, Paremata. General: Maine to Massachusetts in the sublittoral (parent species).

One specimen, probably from the sublittoral since it was in the drift, is tentatively assigned as a variety of *C. laetevirens*. The only difference from the species is that the diameter of the filaments does not change from base to apex. The regularity of filament diameter is marked by the varietal name. In its measurements this plant is close to *C. flagelliformis*, recorded from S. Africa and Tristan da Cunha, but it differs in the shorter branches and non-fusion of the lowest cell of a branch with the adjacent axis cell.

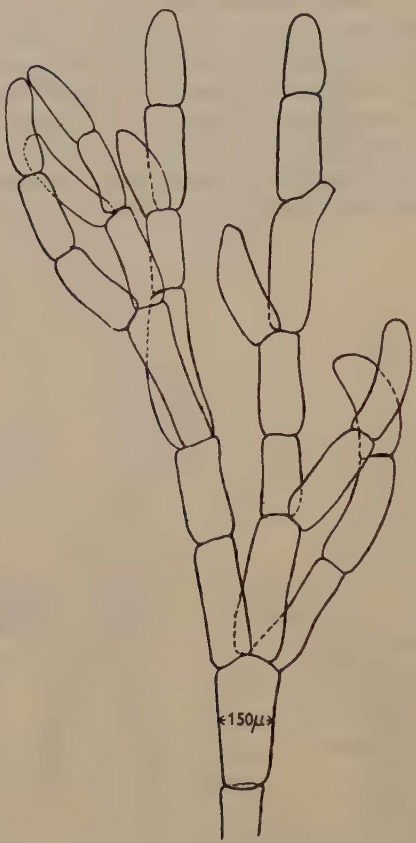

Fig. 113. *Cladophora laetevirens* var. *regularis*.

(25) *Cladophora ceratina* Kütz.

Kütz., *Tab. Phyc.* **4**, tab. 13, fig. 2, 1854; Taylor, *Mar. Alg. N.E. N. Amer.* p. 89, 1937 (as *C. crystallina*).

Plant whitish to pale green, vitreous, up to 3 dm. long, soft, flaccid; filaments lax, intricate, more or less richly di-trichotomously branched, branches erect or spreading, the primary branches 80–140μ thick; branchlets 25–50μ dia., erect or patent, upper branchlets verticillate or alternately secund; cells cylindrical, 4–12 times longer than broad. (Fig. 114.) V.W.L. 130 as *C. sp. incerta.*

DISTRIBUTION. Local: Russell, Aorere Bay, Portobello, St Clair. General: Atlantic, North Sea, Mediterranean, South Australia.

This species is marked in the dried state by the light colour and silky gloss.

(26) *Cladophora repens* (J. Ag.) Harv. f. *tenuis* Hamel.

Harv., *Phyc. Brit.* pl. 236, 1849–51; Kütz., *Tab. Phyc.* **4**, tab. 70, fig. 2, 1854; Hamel, *Chlor. Côtes françaises*, p. 52, 1930.

Thallus caespitose, forming a pulvinate cushion up to 3 cm. dia., velvety; filaments hair-like, flexuous, 60–150μ wide; branching irregular, dichotomous or ternate below, upper branchlets more or less secund; lower cells 6–8 times as long as wide, upper cells 4–6 times; colour grass green; does not adhere to paper. (Fig. 115.)

DISTRIBUTION. Local: Bay of Islands, Matakana Heads, Rangiputa, Waihau, Orewa. General: Great Britain, France, Mediterranean, South Australia.

This species was named *Cladophora velutina* by V. W. Lindauer (mscr.), but it appears to agree with *C. repens* and in particular with the finer form which has been named f. *tenuis*. It is readily recognized by the pulvinate cushion habit. A form *antarctica* has been described from S. Georgia (Gain, 1912), but it is very different from our plant.

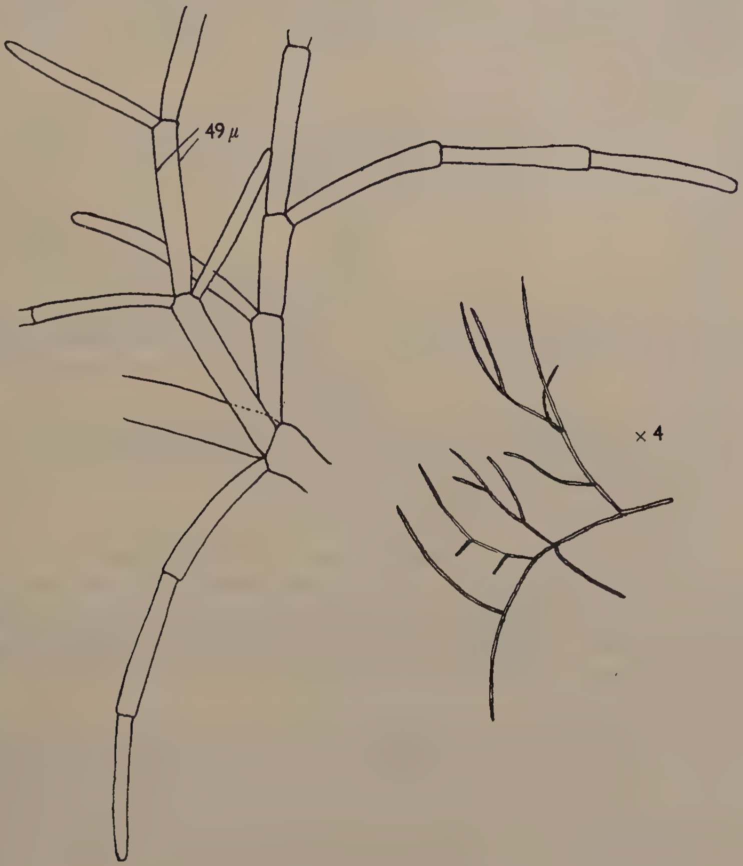

Fig. 114. *Cladophora ceratina.*

(27) *Cladophora frascatii* Collins

Collins, *Green Alg. N. Amer.* 2nd suppl. paper, p. 83, 1928.

Thallus forming a low pulvinate mass, irregular in shape, 2–3 cm. dia.; filaments lax, dilated at apices to 100–120μ wide, dichotomously branched below, irregularly branched above; lower cells 70–100μ dia., upper 60–80μ, 2–5 times longer than broad, somewhat swollen and with constricted nodes; ultimate ramuli 3-celled, nearly all emerging at right angles, often secund on the outer side of a recurved branch. (Fig. 115 A.)

DISTRIBUTION. Local: Rangitoto, Auckland Is. (?). General: Bermuda.

Several samples of this plant have been named by Dr Phinney (mscr.). Of these the one from Rangitoto agrees most closely with the description. I personally feel some doubt about the plants from the Auckland Is. but I have not had the advantage of seeing *C. frascatii* from the northern hemisphere.

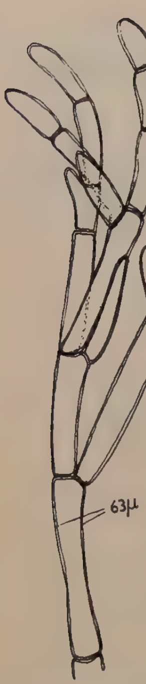

Fig. 115. *Cladophora repens* (J. Ag.) Harv. f. *tenuis* Hamel.

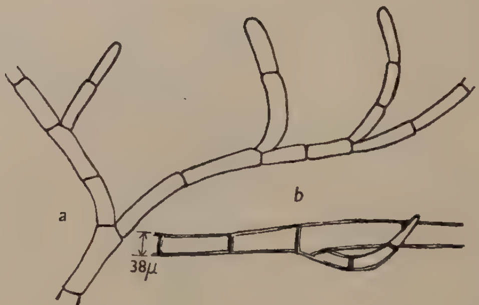

Fig. 115 A. *Cladophora frascatii.*

Chaetomorpha Kütz.

Filaments composed of a single unbranched series of multinucleate cells all, except for a few elongated basal cells, capable of division and reproduction, attached by more or less branched rhizoids, often coalescing, always attached to the substrate at first but later sometimes becoming free; chloroplast a parietal reticulate band with numerous pyrenoids; reproduction by 4-ciliate zoospores or 2-ciliate isogametes; thick-walled akinetes formed from single segments.

Laing (1926) records *Chaetomorpha longiarticulata* J. Ag. and *C. novae-zelandiae* J. Ag. for New Zealand. The descriptions of these two species state that they consist of decumbent and erect filaments. Specimens collected by Berggren and determined by J. Agardh in the Auckland Institute show that neither species belongs to the genus *Chaetomorpha*. A study of the two species by the present author (Chapman, 1952) has resulted in the creation of a new genus, *Rama* (p. 464).

1.	Attached.	2
	Free living for most of life.	*C. linum*
2.	Filaments expanding distinctly from the base to apex.	*C. darwinii*
	Filaments of same width for most of length.	3
3.	Filaments 300–600μ wide.	4
	Filaments less than 300μ wide.	5
4.	Cells 300–600μ wide, basal cell short.	*C. melagonium*
	Cells 450–550μ wide, basal cell long.	*C. pacifica*
5.	Cells as long as broad or slightly shorter.	*C. aerea*
	Cells longer than broad.	6
6.	Filaments 270–300μ.	*C. aureola*
	Filaments less than 200μ.	7
7.	Filaments 75–180μ, cells 1½–2½ times as long as broad.	*C. pallida*
	Filaments 150–170μ, cells usually 2¼–3 times as long as broad.	*C. elongata*

(1) *Chaetomorpha darwinii* (Hook.) Kütz.

J. Ag., De Alg. Nov. Zel. Mar. 2, 1877; Hook., *Fl. Antarct.* **2**, 493, pl. 192, fig. 1, 1847 (as *C. clavata* var. *darwinii*); Harv. in Hooker, *Fl. Nov. Zel.* **2**, 263, 1855; *Handb. N.Z. Flora*, p. 719, 1867; Laing, *Trans. N.Z. Inst.* **57**, 134, 1926.

Plants 5–14 cm. long, up to 2 mm. wide at the apex, attenuate to the base; cells often in pairs, the lower slightly longer than broad, the upper almost spherical, much constricted at the septa; adheres well to paper. V.W.L. 177.

DISTRIBUTION. Local: Pihama, Houghton Bay, Titahi Bay, Ohiro Bay, Runaround Bay, Moa Pt., Kaikoura, Patarau, Gore Bay, Timaru, Banks Peninsula, Taieri Beach, Westport, Chalky Is., Warrington, Blackhead, Gough's Bay, Brighton, Bluff, Tunnel Beach, St Clair, Papanui, Stewart Is. General: New Zealand, Tasmania, South Australia, Kerguelen Is.

This species is a cold water form since it is not found in the northern parts of New Zealand. The typical plants are not unduly long and are markedly swollen towards the apices. Apart from the typical form of the species it appears to exist in three other forms and a variety.

Chaetomorpha darwinii f. **elongata** form.nov.

Planta 15–37 cm. alta, expansa lente ad apicis.

Plants longer than the parent species, 15–37 cm. long, with narrow cells at the base and expanding more slowly towards the apex. Type specimen in herb. Laing from Gore Bay.

DISTRIBUTION. Local: Pihama, Gore Bay, Patiti Pt. Endemic.

The plants are fully mature as empty cells after discharge of swarmers can be seen. It is probable that the form is produced under conditions of excessive exposure.

Chaetomorpha darwinii f. **stricta** form.nov.

Planta 4–11 cm. longa, stricta, cellulis superioribus strictis.

Plants 4–11 cm. long, thinner than the parent species, the upper cells not being so swollen. (Pl. 38.) Type specimen in herb. Laing from Akatore.

DISTRIBUTION. Local: Ocean Beach, Lyall Bay, Akatore, Goose Bay, Green Is. Endemic.

It is possible that here we have a separate species but the plants do have the cells in pairs and there is the gradual expansion to the apex.

Chaetomorpha darwinii var. **chathamensis** var.nov.

Plantis perlongis, cellulis ad apicem valde paulatim augescentibus; cellulis genitalibus sine ordine existentibus, haud regulariter ab apice ad basim procedentibus.

Plants very long, 17–40 cm., swelling very gradually to the dilated apices; reproductive bodies appearing to escape from any intermediate cell and not from the apex downwards. Type P.R.B. no. 52,144, Chatham Is.

DISTRIBUTION. Local: Chatham Is. Endemic.

Laing (mscr.) called this var. *longiarticulata*, thinking it was comparable with Agardh's *C. longiarticulata*. This, however, is not justified. Although this may be a separate species the differences could be due to isolation. For the present it is regarded as more satisfactory to treat it as a variety.

(2) *Chaetomorpha melagonium* (Web. & Mohr.) Kütz.

Harv., *Phyc. Brit.* pl. 99A, 1849–51 (as *Conferva melagonium*); Newton, *Handb. Brit. Seaw.* p. 92, 1931.

Filaments aggregated into tufts or scattered, erect, coarse, stiff, dark green, 20–60 cm., attached by short stout rhizoids; filaments 300–700μ dia., 1–2 times as long as broad; basal cells slightly attenuate below, elongate; does not adhere well to paper.

Chaetomorpha melagonium var. **novae-zelandiae** var.nov.

Filamentis 450–600μ, cellulis ¾–1-cies longioribus quam latioribus.

Filaments 450–600μ, cells ¾–1 times as long as broad. (Fig. 116*c*.) Type specimen in herb. Laing from Kuri Bush.

Distribution. Local: Scott's Pt., Rangitoto, Te Kaminaru, Kuri Bush, Island Bay, Stewart Is. Endemic.

General: Parent species in N. Pacific and N. Atlantic.

It is possible that this variety, which is the form in which the plant occurs in New Zealand, should be treated as a new species. Until the genus has been monographed it is considered better to leave it as a variety of the well-known species.

(3) *Chaetomorpha aerea* (Dillw.) Kütz.

Harv. *Phyc. Brit.* pl. 99B, 1849–51 (as *Conferva aerea*); Newton, *Handb. Brit. Seaw.* p. 92, fig. 60, 1931; Hooker, *Handb. N.Z. Flora*, p. 917, 1867.

Filaments rigid, erect, dark green, becoming yellowish with age, almost cylindrical throughout, slightly attenuate towards the base, attached by rhizoids that later coalesce into a more or less solid disk; filaments 125–300μ or more diameter, cells about as long as broad or slightly shorter, becoming almost spherical when fertile; wall hyaline, thick, sometimes lamellate; does not adhere well to paper. (Fig. 116*a*, *b*.) V.W.L. 2.

Distribution. Local: Bay of Islands, Orewa, Arran, Pohutakawa Flat, Whitianga, Gt Barrier Is., Piha, Huia, Whareponga, Ahuriri lagoon, Cape Egmont, Mikotahi, Moa Pt, Houghton Bay, Titahi Bay, Lyall Bay, Kaikoura, Timaru, Akatore, Riverton, Lawyers Head, Brighton, Bluff, St Clair, Tunnel Beach (Dunedin) and probably elsewhere. General: All warm and temperate seas.

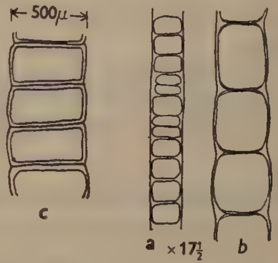

Fig. 116. *a*, *b*, *Chaetomorpha aerea*; *a*, young thread; *b*, old thread. *c*, *C. melagonium* var. *novaezelandiae*. (*a*, *b*, after Setchell and Gardner).

(4) **Chaetomorpha aureola** sp.nov.

Plantis adhaerentibus, ad 20 cm. longis, in fasciculis crescentibus, mollibus, pallido-viridibus, in aureo-virides arescentibus, per cellulam basalem elongatam adhaerentibus, 270–300μ dia., cellulis 1½–3-cies longioribus quam latioribus, septis intercellularibus per crassationem manifestam ad septa maturiora conspicue constrictam distinctis.

Plants attached, up to 20 cm. long, growing in tufts, soft, pale green, turning golden green on drying, attached by an elongated basal cell, 270–300μ wide; cells 1½–3 times as long as broad, septa between cells characterized by a pronounced I-thickening, markedly constricted at the older septa; adheres moderately well to paper. (Fig. 117.) Type P.R.B. Herbarium, no. 69,206, from Green Island.

Distribution. Local: Russell, Lawyers Head, Muriwai, Campbell Bay, Mairangi Bay, Hauturu, Taylor's Mistake, Riverton, Warrington, Brighton, St Clair, Green Is., Stewart Is., Bluff, Te Kaha. Endemic.

In many respects this species is very like *C. aerea* in its measurements, especially in the lower parts of the filaments. The older parts of the filaments are very typical with the elongated cells, the I-thickenings at the septa and the constrictions at the older septa.

These older septa are nearly always covered with an epiphytic growth of *Entocladia cingens* (p. 435). It is possible that this species occurs outside of New Zealand and has been confused with *C. aerea.*

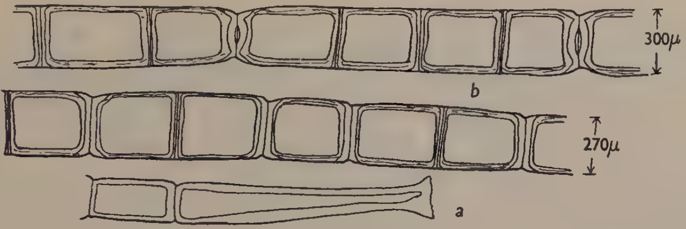

Fig. 117. *Chaetomorpha aureola*: *a*, base; *b*, part of threads.

(5) **Chaetomorpha pallida** sp.nov.

Plantis adhaerentibus, in fasciculis, ad 8 cm. longis, ad basim fusco-viridibus, ad perpallido-fulvas per maiorem partem filamenti arescentibus, filamentis 75–180μ latis, cellulis 1½–2½-cies longioribus quam latioribus; iunctura per cellulam basalem elongatam disco praeditam.

Plants attached, in tufts, up to 8 cm. long, dark green at the base, drying to a very pale yellow over most of the filament; filaments 75–180μ wide, cells 1½–2½ times as long as broad; attachment by an elongated basal cell with a disk; adheres well to paper. (Fig. 118 I.) Type P.R.B. no. 69,204 from Island Bay.

DISTRIBUTION. Local: Long Beach, Island Bay. Endemic.

This species is only represented in material collected by Mr Scarfe, but it differs so markedly from other forms that it is clearly a separate entity.

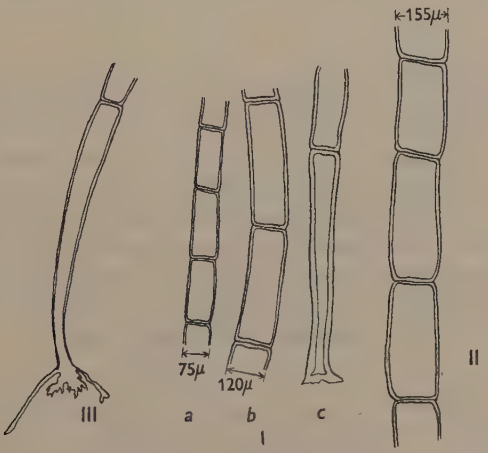

Fig. 118. I. *Chaetomorpha pallida*: *a*, *b*, part of thread; *c*, basal cell. II. *C. elongata*. III. *C. pacifica*: basal cell. (After Börgesen.)

(6) **Chaetomorpha elongata** sp.nov.

Filamentis adhaerentibus per cellulam non valde elongatam, forsitan postea liberatis, intertortis, mollibus, pallido-viridibus, 150–170μ dia., cellulis 1½–3-cies, plerumque 2¼–3-cies longioribus quam latioribus, ad septa constrictis.

Filaments attached, attachment cell not much elongated, possibly becoming free later, entangled, soft, light green, 150–170μ dia., cells 1½–3, usually 2¼–3 times as long as broad, constricted at the septa, does not adhere well to paper. (Fig. 118II.) Type specimen in herb. Laing, from Pile Bay.

Distribution. Local: Pile Bay, Lyttelton, Island Bay. Endemic.

(7) *Chaetomorpha linum* (Muell.) Kütz.

Harv., *Phyc. Brit.* pl. 150A, 1849–51; Newton, *Handb. Brit. Seaw.* p. 91, 1931; Laing, *Trans. N.Z. Inst.* 57, 134, 1926; J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877.

Filaments free-living, setaceous, loosely intricate, long, fresh-green, flexuose, 100–300µ dia., cells 1–2 times as long as broad, occasionally shorter, cylindrical or barrel-shaped; does not adhere to paper. (Fig. 119II.)

Distribution. Local: Orewa, Rangitoto, Motuihi, Tauranga, Te Kaha, Te Kaminaru, Timaru, Tairoa Heads, Sumner, Macandrew Bay, St Clair, Otago Harbour, Stewart Is., Porirua and probably elsewhere. General: N. Atlantic, Mediterranean, Red Sea, Australasia, Kerguelen.

This species occurs in great masses of curled filaments in shallow bays and in pools.

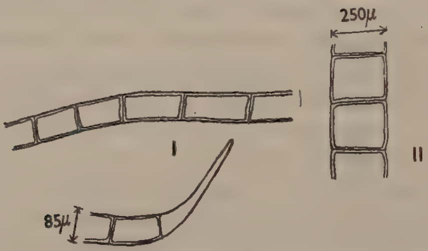

Fig. 119. I. *Lola litorea*. II. *Chaetomorpha linum*.

(8) *Chaetomorpha pacifica* Kütz.

Kütz., *Sp. Alg.* p. 379, 1849.

Filaments 450–550µ wide, fasciculate, erect, lower part cartilaginous, upper flaccid; upper articulations quadrate, the lower cells 16–24 mm. long. (Fig. 118III.)

Distribution. Local: Waitara, Taranaki. General: Indonesia, Australia.

It is possible that this species is synonymous with the Panamanian *C. antennina* which has also been recorded in the American Pacific. In view of the discontinuous distribution, the two species are retained as separate entities here and they obviously form a vicarious pair. Börgesen (Mauritius) gives very big values for the long basal cell of *L. antennina* which are not shown by the N.Z. material. Levring (1941) makes *C. antennina* very polymorphic and he includes *C. pacifica* in the assemblage.

Lola A. & G. Hamel

Filaments 20–100µ dia., in tangled masses, free floating, rarely attached, lateral rhizoidal outgrowths very rare; cells with 5–20 or more nuclei per cell, small, parietal.

The genus *Lola* contains former species of both *Rhizoclonium* and *Chaetomorpha* which lie on the borderline between the two genera. *Lola capillaris* and *L. tortuosa* have frequently been confused in the past. *L. implexa* and *L. tortuosa* differ from species of *Rhizoclonium* in the general absence of rhizoidal outgrowths.

1. Filaments less than 40µ dia. 2
Filaments more than 40µ dia. 4

2. Filaments attached by a disk of coalescent rhizoids. *L. californica*
Filaments free living. 3

3.	Filaments 18–30μ, cells $1\frac{1}{2}$–2 times as long as broad.	*L. implexa*
	Filaments 30–36μ, cells 1–6 times as long as broad.	*L. tortuosa*
4.	Cells $1\frac{1}{2}$–2 times as long as broad.	*L. litorea*
	Cells 2–3 times as long as broad.	*L. capillaris*

(1) *Lola implexa* (Dillw.) Hamel

Harv., *Phyc. Brit.* **1**, pl. 54B, 1849; Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 183, 1920 (all as *Rhizoclonium implexum*); Hamel, *Chlor. Côtes françaises*, p. 118, 1930.

Filaments yellowish or light green, forming a fleecy layer; cells 18–30μ dia., $1\frac{1}{2}$–$2\frac{1}{2}$ times as long as broad; rhizoidal branches very few, more commonly absent, when present non-septate and continuous with the parent cell. (Fig. 124 III.) V.W.L. 127.

DISTRIBUTION. Local: Houhora salt marsh, Orongo Bay, Paihia, Waitangi, Waiwera, Orewa, Howick, Cape Rodney, Noises, Arran, Oneroa, mud of salt marshes and mangrove swamps (Auckland), Piha, Raukura Pt., Fletcher's Bay, Lake Grassmere, Godley Hd, Portobello hatcheries, Long Is., Hooper's Inlet, Chatham Is., probably elsewhere. General: Europe, North America (east and west coasts).

Although this species is primarily a northern hemisphere form, the plants found agree with the description and with European material.

(2) *Lola tortuosa* (Dillw.) comb.nov.

Dillwyn, *Brit. Conf.* p. 46, pl. 46, 1805; Setchell & Gardner, Mar. Alg. Pac. N. Amer. I, Chlorophyceae, p. 186, 1920; Chapman, *Rhodora*, **41**, 19, 1939 (all as *Rhizoclonium tortuosum*).

Filaments rigid, crispate and contorted, dark green; cells 30–36μ dia., 1–6 times as long as broad, average $1\frac{1}{2}$ times, rhizoidal outgrowths few, more usually absent. (Fig. 125, I.)

DISTRIBUTION. Local: Parakino Bridge, Rawene, Frenchmen's Creek, Leigh, Orewa, Stanmore, Cunning Cove, Lake Grassmere, Stewart Is., Chatham Is., Whakataki, Porirua. General: Europe, North America.

Some previous authors have confused *Lola* (*Rhizoclonium*) *tortuosa* with *L.* (*Chaetomorpha*) *capillaris*, but it seems clear that there are two separate species (Chapman, 1939).

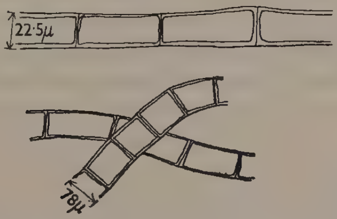

Fig. 120. Above: *Lola californica*. Below: *L. capillaris*.

(3) *Lola californica* (Collins) comb.nov.

Collins, Green Alg. N. Amer. p. 245, 1909.

Filaments attached by a small disk formed of short, stout, coalescent rhizoids, erect, straight or flexuous, of uniform diameter throughout, not constricted at the dividing walls, 20–40μ dia., cells 1–2 rarely 3–4, times as long as broad. (Fig. 120.) V.W.L. 127.

DISTRIBUTION. Local: Long Beach. General: South California.

Although this record gives a very wide discontinuous distribution for the species it is probable that detailed search in the Pacific will show that it has a general Pacific distribution.

(4) *Lola capillaris* (Kütz.) Hamel

Harv., *Phyc. Brit.* pl. 54 A, 1849–51 (as *Conferva tortuosa*); Taylor, *Mar. Alg. N.E. Coast N. Amer.* p. 83, 1937 (as *Rhizoclonium tortuosum*); Hamel, *Chlor. Côtes françaises*, p. 120, 1930.

Filaments rigid, slender, much curled and twisted, forming a broad, closely interwoven stratum; cells 2–3 times as long as broad, 40–100μ (average 60–70μ) dia.; chloroplast dark green; does not adhere well to paper. (Fig. 120.) V.W.L. 305 as *Conferva tortuosa*.

Distribution. Local: Bay of Islands, Rangitoto, Porirua and probably elsewhere in mangrove swamps and on salt marshes. General: Europe, Adriatic, North America, Canaries, Kurile Is.

This species is larger in its measurements than *Lola tortuosa* with which it has often been confused (Chapman, 1939).

(5) *Lola litorea* (Cooke) comb.nov.

Newton, *Hand. Brit. Seaw.* p. 91, 1931; Harv., *Phyc. Brit.* pl. 333, 1849–51 (as *Chaetomorpha litorea*).

Filaments unattached, except possibly in the early stage, entangled, soft and rather delicate, light green, 45–150μ dia., filaments of the same mass variable in width, cells $1\frac{1}{2}$–2 times as long as broad; does not adhere to paper. (Fig. 119 I.)

Distribution. Local: Hobson's Bay, Rosebank, Rangitoto, Waiuku Road, Island Bay. Paremata sand flat, Godley Hd, Shag Pt (Otago), Stewart Is. General: Europe.

This species differs from the preceding one in the paler colour and also in the length of the cells. It is probably more widely distributed than present data suggest.

Rama Chapm.

Filaments prostrate, tangled, formed of a single series of cells, branched very sparsely at the base, with few rhizoidal outgrowths of single cells; chloroplast reticulate, parietal, with numerous pyrenoids.

This genus has been created to include three species with sparse branching like a *Cladophora* but with rhizoidal outgrowths like a *Rhizoclonium*. The species are not well known and the method of reproduction has not been studied. It contains two species that J. Agardh (1877) described from New Zealand and placed in the genus *Lychaete* (*Chaetomorpha*). De Toni (1889) transferred these species, because of the branching, to *Cladophora*. The degree of branching is so slight and so restricted that they are unlike any other species of *Cladophora*. The species with nearest affinity appears to be *C. verticillata*.

1.	Filaments less than 50μ dia.	*R. longiarticulata*
	Filaments more than 50μ dia.	2
2.	Filaments 75–95μ dia.	*R. novaezelandiae*
	Filaments 110–130μ dia.	*R. antarctica*

(1) *Rama longiarticulata* (J. Ag.) Chapm.

De Toni, *Syll. Alg.* **1**, p. 332, 1889 (as *Cladophora longiarticulata*); J. Ag., De Alg. Nov. Zel. Mar., p. 2, 1877 (as *Lychaete longiarticulata*); Laing, *Trans. N.Z. Inst.* **57**, 134, 1926; Chapman, *Trans. Roy. Soc. N.Z.* **80**, 56, 1952.

Plant decumbent, attached at first by rhizoids, then free-floating; rhizoids few at the base, filaments simple, very long, capillary, cells 33–40μ wide, 4–8 times longer than broad; light green; does not adhere to paper. (Fig. 121.)

Distribution. Local: Three Kings Is., Banks Peninsula, Chatham Is., Stewart Is. Endemic.

This species appears to lie on the borderline between *Chaetomorpha* and *Rhizoclonium*. There is no branching in the specimen examined, although such is described by Agardh. The attachment rhizoids have some similarity to those of *Rhizoclonium* but they are restricted in their position. The species is much less like a *Rhizoclonium* than *R. novaezelandiae* and *R. antarctica*.

(2) *Rama novaezelandiae* (J. Ag.) Chapm.

De Toni, *Syll. Alg.* **1**, 332, 1889 (as *Cladophora novae-zelandiae*); J. Ag., De Alg. Nov. Zel. Mar. p. 2, 1877 (as *Lychaete novaezelandiae*); Chapman, *Trans. Roy. Soc. N.Z.* **80**, 56, 1952.

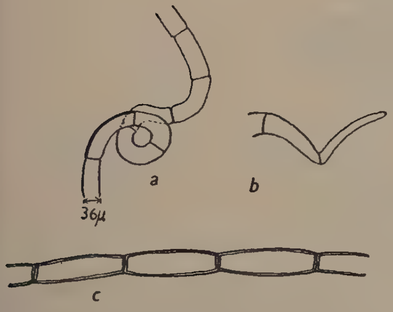

Fig. 121.

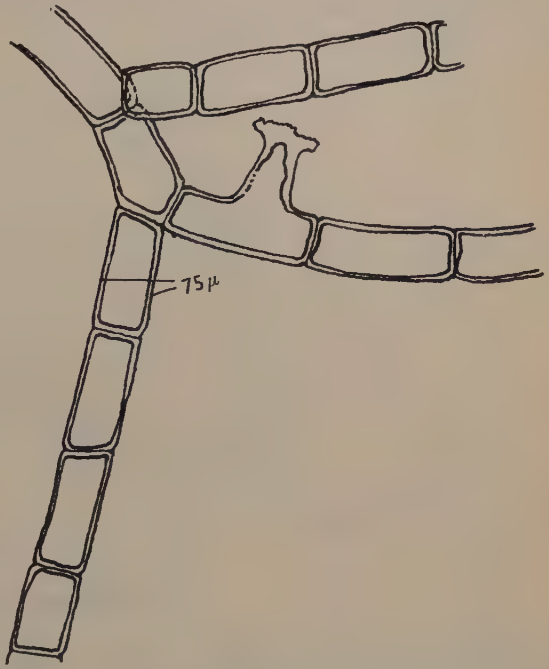

Fig. 122.

Fig. 121. *Rama longiarticulata*: *a*, basal region; *b*, rhizoid; *c*, terminal portion of filament.

Fig. 122. *Rama novaezelandiae*: basal region with rhizoid and branching.

Thallus caespitose, decumbent, attached at first, then floating; lower filaments prostrate, with rhizoidal branches, sparsely branched, branches very long, rarely re-branched and with occasional rhizoidal outgrowths; cells 75–95μ wide, $1\frac{1}{2}$–$2\frac{1}{2}$ times as long as broad, walls thick. (Figs. 122, 126*b*.)

Distribution. Local: Russell, Akaroa Hds., Allen's Beach, Otago, Warrington, Tunnel Beach (Dunedin), and probably elsewhere. Endemic.

The problem of this species was solved by the discovery of a specimen identified by J. Agardh in the herbarium of the Auckland Institute. Until this specimen was found the author was of the opinion that *Rhizoclonium hookeri* existed in a simple and branched form. It now appears that *R. hookeri* has rather narrower filaments and is unbranched, whilst this species has broader filaments (75–95μ as against 47–70μ) and is branched at the base. The presence of the unicellular rhizoidal branches would seem to remove it from the genus *Cladophora*, where it was placed by De Toni, though in possessing branches and rhizoids it is approaching members of the subgenus *Spongomorpha*. It differs from species of *Spongomorpha* in being very loose.

(3) *Rama antarctica* Chapm.

Chapman, *Trans. Roy. Soc. N.Z.* **80**, 57, 1952.

Filaments rigid, sometimes attached by a modified colourless basal cell, very dark green, becoming brownish when dry, loosely intertwined, branched near the base; cells 110–130µ dia., 1–1½ times as long as broad, walls 15–22µ thick, slightly lamellate; rhizoidal branches present, unicellular, arising from parent cell, very short, often attached to a second filament; does not adhere to paper. (Fig. 123.)

Distribution. Local: Snares, Auckland Is., Campbell Is. Endemic.

This species is close to *Rhizoclonium hookeri* from which it differs by its greater size and coarseness. There is also the branching of the filaments and the habit of the rhizoids of attaching themselves to other filaments. The distribution of the species shows that it is quite clearly a subantarctic form.

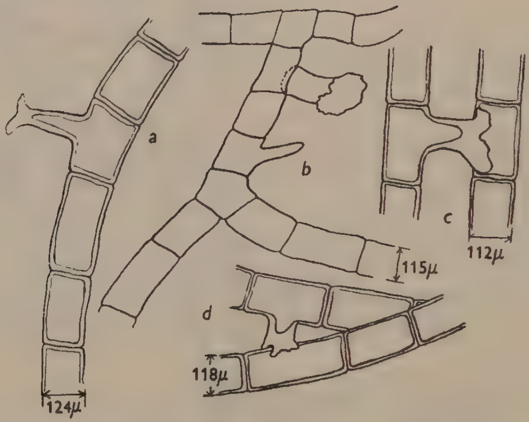

Fig. 123. *Rama antarctica*: *a*, rhizoid; *b*, branched thallus; *c*, *d*, filaments united by rhizoids.

Rhizoclonium Kütz.

Filaments prostrate, formed of a single series of cells, unbranched, simple or occasionally slightly branched, or with few to many rhizoidal branchlets composed of one to few cells; cells usually with more than one nucleus; chloroplast reticulate, parietal, with numerous pyrenoids; multiplication by fragmentation and by akinetes; reproduction by 2-ciliate zoospores.

The species of *Rhizoclonium* are readily distinguished from *Chaetomorpha* when rhizoids are present. In the absence of rhizoids, the only character is the cylindrical nature of the cells as against the barrel-shaped cells of *Lola*. Thus *L. capillaris* could be taken for a *Rhizoclonium*, and in the absence of rhizoids *R. hookeri* could be taken for a *Lola*. There is little doubt that *Rhizoclonium*, *Lola*, *Rama*, *Chaetomorpha* and *Cladophora* are closely allied. *Rama antarctica* and *R. novae-zelandiae* with their branched habit show an affinity to *Cladophora*, whilst *Lola tortuosa* and *Rhizoclonium hookeri* show an affinity to *Chaetomorpha*.

1.	Filaments rigid, 47–70µ, dark green, rhizoids scarce.	*R. hookeri*
	Filaments flaccid, less than 40µ dia., light green.	2
2.	Rhizoidal branches scarce or absent.	*R. kerneri*
	Rhizoidal branches frequent	3
3.	Rhizoidal branches 1–3 septate, walls thin	4
	Rhizoidal branches 5–7 septate, walls thick	*R. elongatum*
4.	Filaments 18–26µ dia.	*R. riparium*
	Filaments 40µ dia.	*R. curvatum*

(1) *Rhizoclonium riparium* (Roth) Harv.

Harv., *Phyc. Brit.* 2, pl. 238, 1849–51; Setchell & Gardner, Mar. Alg. Pac. N. Amer. Chlorophyceae, p. 182, 1920.

Filaments pale green, expanded on substrate, flexuous, intertwined into a fleece; cells 18–26μ dia., usually 1–2 times as long as broad, walls thin; rhizoidal branches frequent, often 2- to 3-celled. (Fig. 124I.) V.W.L. 306.

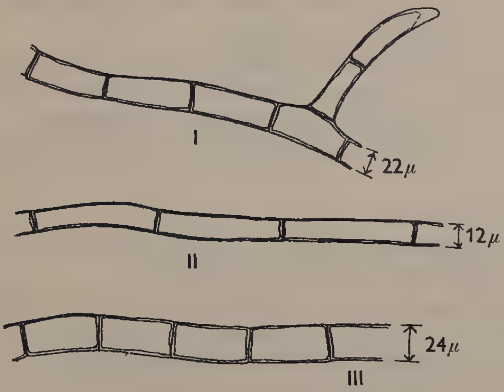

Fig. 124. I. *Rhizoclonium riparium*. II. *R. kerneri*. III. *Lola implexa*.

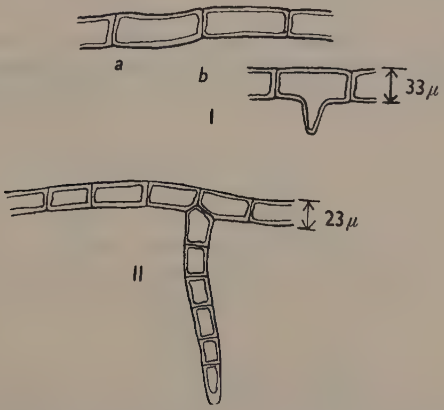

Fig. 125. I. *Lola tortuosa*. II. *Rhizoclonium elongatum*.

Distribution. Local: Orongo Bay, Brick Bay, Waitangi, Frenchman's Creek, Stanmore, Orewa, Whangaparaoa Hds, Piha, Huia, Narrow Neck, Palm Beach, Coromandel, Whitianga, Needle Point, Mouth of Kaikorai, Tunnel Beach, Port Chalmers, Otago Peninsula, Chatham Is., Dusky Sound, Eastbourne, probably widespread. General: Atlantic North America, Alaska to Central California.

(2) **Rhizoclonium elongatum** sp.nov.

Filamentis flavo-viridibus, flaccidis, in vellus intertortis; cellulis 18–26μ dia., 1–1$\frac{3}{4}$-cies longioribus quam latioribus, parietibus 4μ crassis, non lamellatis; ramis rhizoidalibus frequentibus, e 6–7 cellulis constantibus.

Filaments yellowish green, flaccid, intertwined into a fleece; cells 18–26μ dia., 1–1$\frac{3}{4}$ times as long as broad, walls 4μ thick, not lamellate; rhizoidal branches frequent, composed of 6–7 cells; adheres imperfectly to paper. (Fig. 125II.) Type in Herb. Auckland Inst., from Tauranga.

Distribution. Local: Narrow Neck. Tauranga. Endemic.

This species is very similar to *R. riparium* but is characterized by the very long rhizoidal branches. It is probably more widespread in the Dominion.

(3) *Rhizoclonium kerneri* Stockm.

Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 185, 1920.

Filaments pale yellowish green, intertwined; cells 10–14μ dia., 3–7 times as long as broad; rhizoidal branches absent. (Fig. 124II.)

Distribution. Local. With other algae in mangrove swamp, Russell, Tarpeka, Orongo Bay, Howick, Lake Grassmere, Island Bay, Porirua and probably elsewhere. General: Vancouver Is., Mediterranean, Atlantic, West Indies.

This species is characterized by its very slender threads and may well be overlooked.

(4) *Rhizoclonium hookeri* Kütz.

Kütz., *Tab. Phyc.* 3, tab. 67, fig. 2, 1853 (as *R. ambiguum* and *R. africanum*); Laing, *Trans. N.Z. Inst.* 57, 134, 1926 (as *R. africanum*).

Filaments rigid, dark green, simple, intertwined to form a fleecy layer; cells 47–70μ dia., 1–2 times as long as broad; walls thick, lamellate; rhizoidal branches rare. (Fig. 126*a*.)

Distribution. Local: Stanmore, St Heliers, Noises, Rangitoto, Raukma Pt, Fletcher's Bay, Whangaparapara, Punakaiki, Oahoa, Akatore, Moeraki, mouth of Kaikorai, Island Bay, Dunedin, Chatham Is., Snares, Auckland Is., Campbell Is., Cape Foulwind, Porirua, Raglan and probably elsewhere. General: Australia, East Indies, New Zealand, Malaya, Kerguelen, Fuegia, S. Africa.

This species is unmistakable because of its coarseness and large size. In appearance it is very similar to *R. novae-zelandiae*. In the past, this species has also been described as *R. africanum* and *R. ambiguum*, but they all appear to be identical.

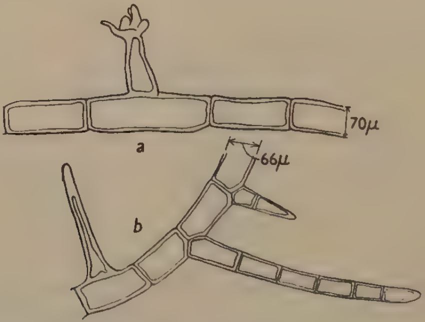

Fig. 126. *a*, *Rhizoclonium hookeri*, *b*; *Rama novae-zelandiae*, branches and rhizoid.

(5) **Rhizoclonium curvatum** sp.nov.

Filamentis mollis, simplicis, ramis paucis, contortis, laxe intertortis; cellulis 40μ dia., $\frac{1}{2}$–1-cies longioribus quam latioribus; ramis rhizoidalibus frequentibus, 1–2 cellulis constante, filamentis media curvatis.

Filaments soft, simple, rarely branched, contorted, loosely intertwined; cells 40μ dia., $\frac{1}{2}$–1 time as long as broad; rhizoidal branches frequent, 1–2 cells long, intervening filament curved. (Fig. 127.) Type specimen in Herb. Auckland Inst., from Manakau.

Distribution. Local: Manakau Harbour by Puketutu Is. Endemic.

This species is characterized by the regular curved segments of the filament between each rhizoidal branch. It appears to be most closely allied to *R. riparium*, from which it differs in cell size.

Hormiscia Fries

Filaments simple, attached at base by rhizoids developed from basal cells; cells multinucleate, chloroplast entire or coarsely reticulate, with few to many pyrenoids; multiplication by akinetes formed by filaments breaking up into individual segments; reproduction by 4-ciliate macrozoospores or microzoospores and biciliate iso- or anisogametes.

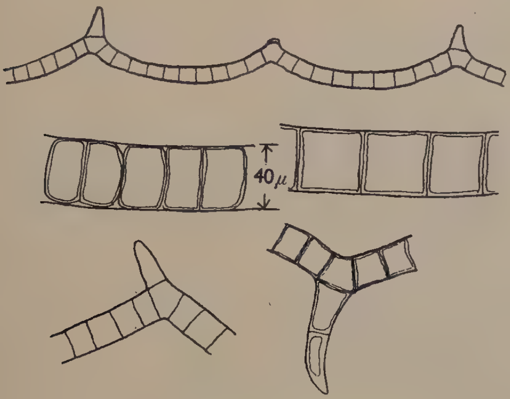

Fig. 127. *Rhizoclonium curvatum.*

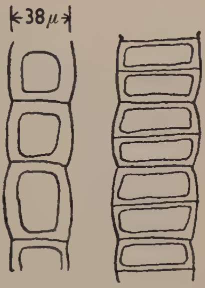

Fig. 128. *Hormiscia penicilliformis.*

Hormiscia penicilliformis (Roth) Fries

Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 191, pl. 9, fig. 4, 1920; Laing, *Trans. N.Z. Inst.* **57**, 136, 1926 (as *Urospora penicilliformis*); De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 88, 1923 (as *U. penicilliformis*).

Filaments dark green, attached by rhizoids from a few of the basal segments, 30–60μ and up to 90μ dia., cells 0·3–2·5 times as long as broad; vegetative cells mostly cylindrical, fertile cells more or less barrel-shaped; chloroplast usually a dense, continuous parietal band, or at times reticulate, pyrenoids relatively few and large. (Fig. 128.)

Distribution. Local: Russell, Narrow Neck (Auckland), Gisborne, Lyttelton. General: North Atlantic, Alaska–Central California, S. America, Falkland Is., Kerguelen, Grahamsland, Crozet Is.

WITTROCKIELLACEAE

Frond consisting of slightly branched, pluricellular, upright filaments, the cells of which can develop unicellular hairs. Cells multinucleate, with green or yellow net-shaped parietal chloroplast, sometimes developing an orange-coloured oil. Reproduction by akinetes or aplanospores, the latter formed in numbers by free division in an aplanosporangium; zoospores and gametes unknown. Only one genus.

Wittrockiella Wille

Filaments embedded forming a cartilaginous expansion or a mat; pluricellular rhizoids produced below, uni-, rarely bicellular hairs sometimes produced above; chloroplast with numerous pyrenoids, aplanosporangia formed from terminal cells or akinetes produced in upper vegetative cells.

(1) *Wittrockiella salina*

Chapman, *Farlowia*, **3** (4), 495, fig. 1, 1949.

Plants microscopic, consisting of short, branched filaments with simple or forked, rhizoidal cells; cells very variable in width and length, ranging from almost quadratic to

6 times as long as broad; chloroplast reticulate; many of the filaments with a 'knee' cell, usually with denser contents, 150–198μ average dia.; reproduction unknown. (Fig. 129.)

DISTRIBUTION. Local: Orongo Bay, Stanmore, Orewa, Te Haruhi Bay, Palm Beach (Waiheke), Whangaparapara. Endemic.

The plant is microscopic and occurs mixed with filaments of other algae.

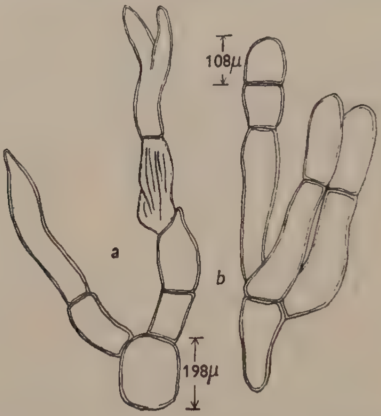

Fig. 129. *Wittrockiella salina.* (After Chapman.)

VALONIACEAE

Frond consisting of a simple or branched coenocyte attached to the substratum by rhizoids, or of a complex septate thallus differentiated into a main axis with branches, cells all multi-nucleate; chloroplasts small, numerous; reproduction by biciliate swarmers or aplanospores.

Cladophoropsis Börg.

Thallus forming cushions on rocks or epiphytic on other algae; plant consisting of branched filaments, branching irregular; branches commonly in open connexion with mother cells as basal wall is absent; chloroplasts disk-like, numerous; cells multinucleate; reproduction by zoospores.

The type species of the genus is *C. membranacea*, which is not represented in New Zealand, but two other endemic species are placed in this genus. In general these two species are intermediate between *Cladophora* and *Cladophoropsis*, especially in that some of the branches are in open connexion with the mother cells, whereas others are not. All three species are similar in habit, forming coarse, cushion-like tufts.

Key to local species

1.	Cells usually more than 10 times longer than broad.	*C. herpestica*
	Cells usually less than 10 times longer than broad.	*C. lyallii*

(1) *Cladophoropsis herpestica* (Mont.) comb.nov.

Kütz., *Sp. Alg.* p. 415, 1849; Mont. *Voy. au Pole Sud.* 1, 6, 1942–5; J. Ag., De Alg. Nov. Zel. Mar. p. 3, 1877 (as *Cladophora herpestica*); Cotton, *Kew Bull. Misc. Inf.* p. 326, 1912; Laing, *Trans. N.Z. Inst.* 57, 133, 1926 (as *Cladophora herpestica*).

Thallus caespitose, up to 2 cm. tall, repent; filaments hair-like, utriculaceous, rigid, 150–375μ wide, wall 14–18μ thick, not distinctly lamellate; branching irregular, upper branches fasciculate; cells up to 15 times as long as broad; colour dark green; does not adhere to paper. (Fig. 130.) V.W.L. 80.

Distribution. Local: Cape Maria, Three Kings Is., Russell, Opua, Waimamuku, Rangiputa, Matakana Heads, Narrow Neck, Huia, Great Barrier, Little Barrier, Raukura Pt, Gannet Rocks, Fletcher's Bay, Arran, St Heliers, Waihau Bay, Pelorus Sound and probably elsewhere. General: Viet Nam.

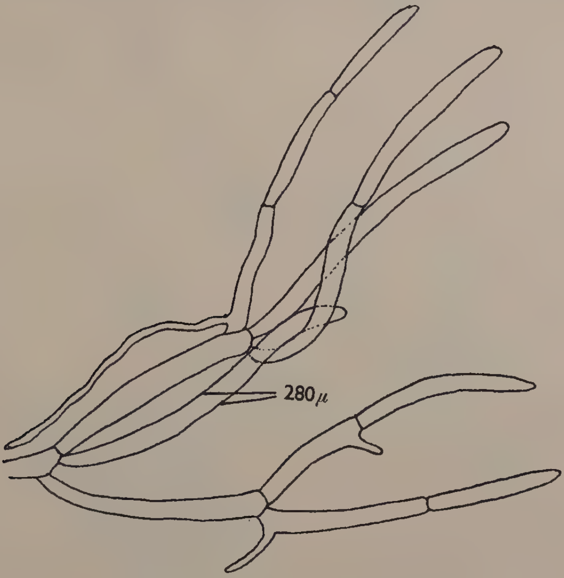

Fig. 130. *Cladophoropsis herpestica.*

(2) *Cladophoropsis lyallii* (Harv.) comb.nov.

Harv. in Hooker, *Fl. Nov. Zel.* **2**, p. 262, tab. 121C, 1855; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926 (both as *Cladophora lyallii*).

Thallus densely pulvinate; filaments up to 2·5 cm. tall, pale to dark green, coarse, rigid, subfastigiate, interwoven, flexuose; branching sparse, alternate or secund, sometimes opposite, patent; apices of branchlets obtuse; cells 200–400μ dia., usually 2–3 times longer than broad, more rarely up to 7 times, constricted at the joints. (Fig. 131.) V.W.L. 253 as *C. membranacea.*

Distribution. Local: Puketeraki, Stewart Is., and probably Antarctic Islands. Endemic. This species is the coarsest of the *Cladophora*-like plants and is readily identified by its moss-like habit and very large cells. *C. herpestica* is a northern species, whereas *C. lyallii* is very distinctly a southern species. The filaments are very much more flexuous than those of *C. herpestica* and the cells are much shorter. Whilst not every branch is in open communication with the mother cell there are sufficient to justify transferring the plant from *Cladophora* to *Cladophoropsis.*

SIPHONALES

Fronds filamentous, simple or variously entangled or interwoven, sometimes producing complex individuals, devoid of septa in the vegetative portions, multinucleate and with numerous small chloroplasts; multiplication vegetative, by non-sexual spores or by iso- or anisogametes; asexual spores usually produced in special sporangia.

1.	Plant microscopic, in shells of molluscs	Ostreobium
	Plant macroscopic.	2
2.	Plants cushion-like, creeping, with no distinctive erect portion.	Codiaceae
	Plants with distinctive erect axes.	3

3. Erect axes filamentous, sparingly and irregularly branched. Derbesiaceae
   Erect axes filamentous with pinnate or radial branching. Bryopsidaceae
   Erect axes compound or non-filamentous. 4
4. Erect axes compound, composed of numerous siphonaceous filaments. Codiaceae
   Erect axes composed of a single siphonaceous filament, simple or branched. Caulerpaceae

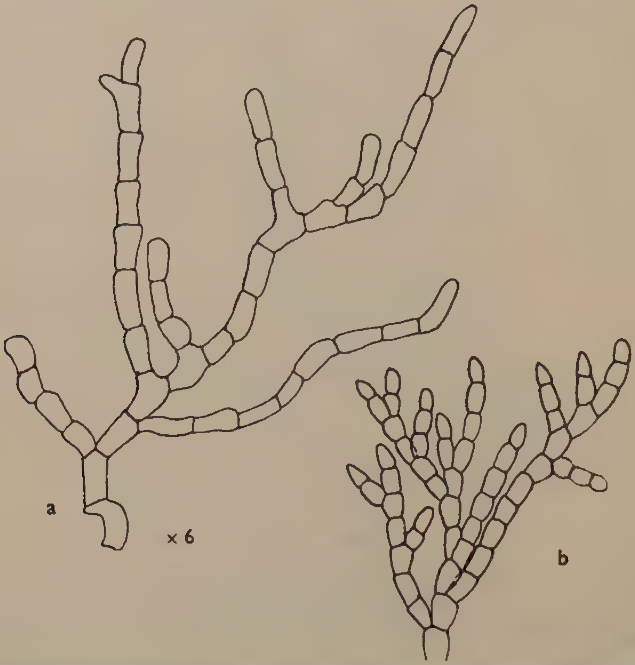

Fig. 131. *Cladophoropsis lyallii.* *a*, part of plant; *b*, Harvey's original drawing reproduced.

PHYLLOSIPHONACEAE

Plants endophytic or endozoic, composed of large oval cells or branched filaments without cross-walls, coenocytic, with many nuclei and disk-like chromatophores without pyrenoids; reproduction by aplanospores produced in great numbers.

Ostreobium Born. & Flah.

Plants filamentous, of much branched and apparently anastomosing coenocytic filaments of very variable form and variable diameter; aplanospores formed in the swollen ends of branches.

(1) *Ostreobium reineckei* Born.

Born., *Bot. Jahrb.* **23**, p. 269, 1896; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926.

Filaments intricately spreading, the ends of the branches consistently free. (Fig. 132*b*.)

DISTRIBUTION. Local: in shells of molluscs, probably generally distributed. General: Mexico.

DERBESIACEAE

Thallus of erect, simple or sparsely branched coenocytic filaments, arising from slender, creeping filaments attached by short, branched rhizoids; chloroplasts small, disk-like, with or without pyrenoids; asexual reproduction by zoospores with a circlet of cilia, produced in lateral, globose to pyriform zoosporangia; sexual reproduction unknown.

Derbesia Solier

Filaments coenocytic, multinucleate, simple or branched with no differentiation of axis and branches; numerous discoid chloroplasts, with or without pyrenoids; zoosporangia borne laterally, globose to pyriform in shape, producing large multiciliate zoospores.

1. Filaments 37–52μ wide.	*D. novaezelandiae*
Filaments 50–70μ wide.	*D. marina*

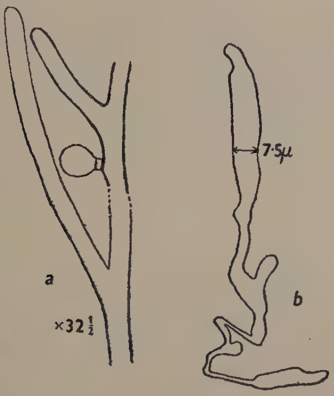

Fig. 132.

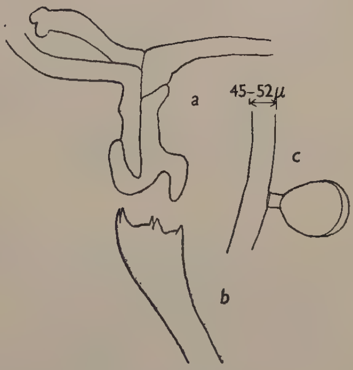

Fig. 133.

Fig. 132. *a*, *Derbesia marina*; *b*, *Ostreobium reineckei*. (*a*, after Setchell & Gardner.)

Fig. 133. *Derbesia novaezelandiae*: *a*, joined filaments; *b*, attachment hooks; *c*, akinete. (After Chapman.)

(1) *Derbesia marina* (Lyngb.) Kjellm.

Setchell & Gardner, Mar. Alg. Pac. N. Amer., Chlorophyceae, p. 165, pl. 15, fig. 3, 1920; Laing, *Trans. N.Z. Inst.* **57**, 133, 1926.

Filaments arising from a creeping base, bright green, 50–70μ dia., partitions forming a short segment, occasionally present near the base of a branch or in the region just above a branch; sporangia ovoid to subspherical 150–250μ long, 90–200μ wide; pedicel 30–70μ long. (Fig. 132*a*.)

DISTRIBUTION. Local: no locality in Laing's list. General: Europe, Alaska to S. California.

This species is recorded in Laing's List (1926), but it is doubtful if it is present. It has been recorded as *D. tenuissima*. It has recently been shown that *D. marina* is the asexual generation of *Halicystis ovalis*. If this is correct then one might well expect to find *Halicystis* around our shores. It is possible that Laing named the following species as *D. marina*, though there is a distinct difference in filament width.

(2) *Derbesia novaezelandiae* Chapm.

Chapman, *Farlowia*, **3** (4), 498, fig. 5, 1949.

Thallus composed of coenocytic filaments, branching irregularly; filaments 37–52μ wide; asexual reproduction by means of zoosporangia 95–102μ wide and 120–150μ long, borne laterally on a single-celled stalk; sexual reproductive organs apparently absent. (Fig. 133.)

DISTRIBUTION. Local: Kermadecs, on *Corallina officinalis* in rock pools, Russell, Waiwera, Stanmore, Cape Rodney, Narrow Neck, Shag Rock, Kaikoura, Noises Is. Gannet Rock. Endemic.

This species is somewhat smaller in its measurements than *D. marina* (*D. tenuissima*) but is rather larger than *D. vaucheriformis*. Apart from these differences, however, one of the most interesting features is the tendency of certain portions of filaments from the same or adjacent plants to become appressed to one another (Fig. 133) and held in position by minute appendages. This may represent a degenerate form of sexual reproduction though no evidence has been seen of zygote formation.

BRYOPSIDACEAE

Thallus generally erect from a more or less extended rhizoidal holdfast; erect axis branched, the branches either continuing like the axis or forming short branchlets of limited growth, never interwoven; thallus coenocytic; chloroplasts numerous, oval to elliptical, each with a single chloroplast; vegetative reproduction by fragmentation; no asexual reproduction; sexual reproduction by conversion of branchlets into gametangia or by the production on the branchlets of lateral gametangia cut off by a basal wall; gametes biflagellate, anisogamous.

Bryopsis Lamouroux

Erect thallus tufted or spreading, with or without more or less evident main axes, much branched or more or less simple; branchlets occurring more or less over the whole plant or restricted to apical portions of the branches; branching radial or distichous; plants diploid, dioecious; sexual reproduction by conversion of branchlets into gametangia; male gametes brownish, female yellowish green.

The species belonging to this genus have proved extremely difficult to handle. Former workers have classed all forms within either *B. vestita* or *B. plumosa*. Collectors such as Mr Laing, Mr Scarfe and Miss Moore have all realized that other species were in fact present. Unfortunately many of the plants do not lend themselves to ready identification after treatment as herbarium specimens. Lack of authentic material from other parts of the Pacific has not assisted the identifications. There is no doubt, however, that New Zealand is extremely rich in species of this genus, many of them new to science, and also some of the species are remarkable for their great size. One might almost suggest that these waters or those of the South Pacific represent the home of the genus or else that, in view of the great number of endemic forms, active evolution is at present taking place around our shores. It is evident also that the entire genus is seriously in need of monographing.

1.	Branching radial.	3
	Branching distichous.	11
	Branching tetrastichous.	*B. tetrasticha*
	Lower branching radial, upper distichous.	2
2.	Branches 410–450μ dia., with rhizoidal outgrowths.	*B. rhizoidea*
	Branches 262–412μ dia., no rhizoids.	*B. pseudoplumosa*
3.	Rhizoidal outgrowths at base of ramuli and lower pinnules.	*B. corticulans* var. *novae-zelandiae*
	Rhizoidal outgrowths rare or only incipient on ramuli.	4
4.	Branches and pinnules delicate, scattered, plants more than 3 cm. long.	5
	Branches and pinnules frequent, plant tufted, less than 3 cm. long.	6
	Branches and pinnules coarse, frequent.	7
5.	Pinnules 37–56μ dia.	*B. otagensis*
	Pinnules 75–100μ dia.	*B. fusca*
	Pinnules 111–160μ dia.	*B. scarfei*
6.	Pinnules 48–53μ.	*B. derbesioides*
	Pinnules 80–110μ.	*B. corymbosa*
7.	Branches pinnate, plume linear.	9
	Branches mainly otherwise, or, if pinnate, plume not linear.	8

8.	Pinnules 150–188μ, main branches without rhizoidal outgrowths.	*B. lindaueri*
	Pinnules 130–150μ, main branches sometimes with rhizoidal outgrowths.	*B. pseudocorymbosa*
9.	Axis and ramuli densely clothed throughout.	**10**
	Axis and ramuli not densely clothed throughout.	*B. duchassaingii*
10.	Ramuli 180–240μ, pinnules 94–150μ.	*B. vestita*
	Ramuli 330–640μ, pinnules 150–225μ.	*B. moorei*
11.	Plants very large, up to 17 cm., and coarse.	*B. canterburyensis*
	Plants smaller.	**12**
12.	Pinnules thin, 75–120μ dia.	*B. plumosa*
	Pinnules broader.	**13**
13.	Pinnules restricted to apex.	**14**
	Pinnules generally scattered.	*B. pseudopennata*
14.	Pinnules 120–188μ, tapering to apex, clothing at least half of ramuli.	*B. olivacea*
	Pinnules 150–188μ, not tapering, clothing much less than half of ramuli.	*B. pennatula*

(1) *Bryopsis vestita* J. Ag.

J. Ag., *Till Alg. Syst.* 8, 30, 1886; J. Ag., De Alg. Nov. Zel. Mar. p. 3, 1877; Laing, *Trans. N.Z. Inst.* **57**, 131, 1926.

Plants ranging in size from 4 to 15 cm. long; main axis very distinct, usually simple, occasionally with one or two branches of a lesser order; axis generally beset throughout its entire length with numerous radially placed ramuli; in older plants, or perhaps at certain seasons, the lower part of the axes may be bare or only carry remains of ramuli; ramuli simple or sparsely divided, 180–242μ broad, beset with numerous pinnules towards the apex; pinnules simple and short, 94–150μ broad; plants light to dark green.

This species appears to exist in several distinct forms, one of which is confined to the Chatham Islands. Two of the other forms may be seasonal phases since one, f. *laxa* appears to occur mostly in the summer, whilst f. *virgata* is more frequent in the winter and spring. Until culture experiments have been carried out in order to determine this point they are regarded as distinct entities. The suggestion that they may be seasonal forms is also supported by the fact that the plants of f. *laxa* are always larger than those of *f. virgata*.

Bryopsis vestita f. **laxa** form.nov.

Plantis 10–15 cm. longis, multos ramulos laxos elongatos ad 2 cm. longos ferentibus; ramulis ex parte axis inferiore plerumque non ramosis, ex parte axis superiore saepe ramosis, plantis saepius pallido-viridibus.

Plants 10–15 cm. long, main axis bearing numerous elongate ramuli up to 2 cm. long; ramuli from lower part of axis generally unbranched, more often branched towards apex of main axis; ramuli beset with pinnules towards apex; plants usually a light green in colour; does not adhere well to paper; occurs principally in December and January. (Pl. 39.) V.W.L. 201. Type specimen in Herb. Auckland Inst. Remainder cotypes.

DISTRIBUTION. Local: Whakataki to Castle Point, Nelson, Lyttelton, Moeraki, Black Head, Riverton, Bluff, Warrington, St Clair, Kaha Pt, Waikouaiti, Portobello, Half Moon Bay, Stewart Is., probably general throughout the South Island. Endemic.

Bryopsis vestita f. **virgata** form.nov.

Plantis 4·5–13 cm. longis, axe primario plerumque simplici, vestito multis ramulis virgatis brevioribus quam in f. *laxa*, planta tota compactiore; colore fusco-viridi.

Plants 4·5–13 cm. long; main axis nearly always simple, clothed with numerous ramuli shorter than those of f. *laxa*, the whole plant having a much more compact appearance; ramuli generally unbranched but clothed throughout most of their length with numerous short pinnules; plants dark green in colour; adheres well to paper; occurs principally from August to December. Type specimen in Herb. Auck. Inst. from Lyttelton.

Distribution. Local: Nelson, Puketeraki, Lyttelton, Timaru, Greymouth, Riverton, St Clair, Akatore, Wycliffe Bay, Tautuku, Bluff Hill, Stewart Is., and probably generally throughout the South Island. Endemic.

Bryopsis vestita f. **brevis** form.nov.

Planta parva, 2·5 cm. longa, similariter ad f. *virgata*.

Similar to f. *virgata* but plants regularly less than 2·5 cm. in length. Type specimen P.R.B. no. 44,076 from Auckland Is.

Distribution. Local: New Plymouth, Greymouth, Auckland Is.

This form may be a response to exposed conditions.

Bryopsis vestita f. **densa** form.nov.

Plantis 3–6 cm. longis, axe simplici vel diviso.

Plants moderate in size, 3–6 cm. long, up to 2 cm. wide in the bushiest part, axis simple or divided, pinnules 150μ dia., arising mainly near apices of pinnae which are 168–206μ dia. (Fig. 134.) Type specimen P.R.B. no. 40,192.

Distribution. Local: Lyttelton.

Differs from other forms in the greater diameter of the pinnules and the rather smaller size of the ramuli and their mode of branching. It is possible that this form may be a separate species, but further work on it is necessary.

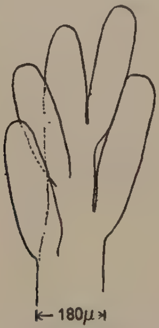

Fig. 134. *Bryopsis vestita* f. *densa*.

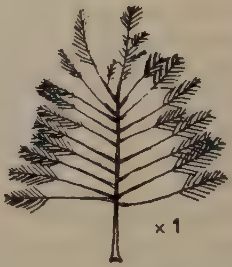

Fig. 135. *Bryopsis plumosa*. (After Setchell & Gardner.)

Bryopsis vestita f. **chathamensis** form.nov.

Parte axis superiore vestita multis ramulis brevibus radialiter dispositis, vestigiis ramulorum talium in parte axis inferiore visibilibus, planta tota incomptiore quam f. *virgata*.

Plants 5–10 cm. long, main axis nearly always simple, sometimes branched towards the apex in a fasciculate fashion, the upper half of the axes clothed with numerous, radially arranged, short ramuli, remnants of such ramuli being visible on the lower half of the axes, the whole plant having a more 'scraggy' appearance than f. *virgata*.

Type specimen P.R.B. no. 69,253.

Distribution. Local: Chatham Islands.

(2) *Bryopsis plumosa* (Huds.) Ag.

Harv., *Phyc. Brit.* **4**, pl. 3, 1851; Kütz., *Tab. Phyc.* **6**, tab. 83, 1856; Harv. in Hooker, *Fl. Nov. Zeal.* **2**, 195, 1855; *Handb. N.Z. Flora*, p. 714, 1867; Laing, *Trans. N.Z. Inst.* **57**, 131, 1926.

Plants ranging in size from 2·5 to 6·5 cm. or more; main axis simple or branched once or twice in smaller plants but with more numerous branches in larger plants; the axis and branches bare below but beset towards the apex by distichous pinnae, themselves with distichous pinnules near the apex, attenuate above and below and later sometimes falling off; pinnae 170–225μ wide, wall 3μ thick, pinnules 75–120μ wide; plant grass green in colour. (Fig. 135.)

This species is characterized by its relatively small size and by the fact that the lower pinnules and pinnae are longer than those at the apex so that the branched frond has a triangular contour.

DISTRIBUTION. Local: Bay of Islands, O'Neill's Beach, Anawhata, Piha, Gt Barrier Is., Gannet Rock, Fletcher's Bay, Whitianga, Mt Mangonui, Cooks Str., Akaroa, Greymouth (?), St Clair, Portobello, Akatore, Otago. General: Europe, Mediterranean, North America, Pacific N. America, South Africa, Australia, Tasmania, New Zealand.

It is possible that more than one form is involved here.

(3) **Bryopsis otagensis** sp.nov.

Plantis 5–10 cm. longis; axe primario non conspicue distincto, plerumque ramoso; ramis 480μ latis, pariete 4μ crasso, irregulariter oriente; ramis et axe primario infra plus minusve nudis, superne vestitis ramulis multis subtilibus disiectis elongatis ad 3 cm. longis, per maiorem partem longitudinis pinnulas perdelicatas elongatas disiectas ferentibus; ramulis 92–150μ latis, basi constrictis, infimis interdum praeditis surculis rhizoidalibus e basi orientibus; pinnulis 37·5–56μ latis, non basi constrictis; ramulis et pinnulis radialiter dispositis, valde irregulariter insertis; planta colore gramino-viridi, ad chartam bene adhaerente.

Plants 5–10 cm. long; main axis not markedly distinct, usually branched; branches 480μ wide, wall 4μ thick, arising in an irregular fashion; branches and main axis more or less bare below but clothed above with numerous slender, scattered, elongate ramuli up to 3 cm. long, which bear very delicate, elongate, scattered pinnules for most of their length; ramuli 92–150μ wide, constricted at the base, the lowest sometimes with rhizoidal outgrowths from the base; pinnules 37·5–56μ wide, not constricted at the base; arrangement of ramuli and pinnules radial but insertion very irregular; plant grass green; adhering well to paper. (Fig. 136; Pl. 40.) Type P.R.B. no. 69,210 from Otago Harbour.

DISTRIBUTION. Local: Muddy bay in Otago Harbour, 1917. Endemic.

This plant was recognized by Mr Scarfe as being a species new to New Zealand and probably also to science. In view of the tendency to produce rhizoidal outgrowths from the base of the pinnules it must be regarded as allied to *B. corticulans* although it is much more slender. It also appears to be closely allied to *B. tenuis* Levring of South Africa.

The species is characterized by the great length of the ramuli and pinnules in relation to their width and also by the delicate character of the whole plant. In appearance it looks very much like *Enteromorpha clathrata* or *E. plumosa*. Other typical features are the constricted bases of the ramuli and the unconstricted bases of the pinnules together with the interrupted nature of their points of origin. Experiments will be necessary to determine whether, if still occurring, this species is valid or is a response of another species to the environment, i.e. is an ecad.

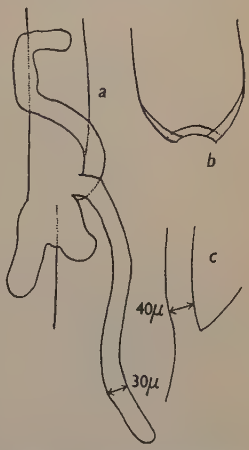

Fig. 136. *Bryopsis otagensis*: *a*, rhizoids at base of lower ramuli; *b*, base of upper branch; *c*, base of apical branchlet.

(4) **Bryopsis rhizoidea** sp.nov.

Plantis 6·5–11·5 cm. longis, axe primario distincto, simplici, ad 1265μ lato, pariete 30μ crasso, dense vestito surculis rhizoidalibus e basibus ramorum primariorum orientibus; ramis primariis 410–450μ latis; pariete 7·5μ crasso, basi constrictis; utroque ramorum ordine radialiter disposito; ramulis infra nudis, superne vestitis pinnulis multis ad basim radialiter dispositis, plus minusve superne distichosis, plumam lineari-lanceolatam formantibus; pinnulis 110–128μ latis, basi constrictis; pinnulis infimis et ramulis seriatim dispositis, praeditis surculis rhizoidalibus e basi orientibus; plantis colore oleagino; axe primario non bene, plumis bene, ad chartam adhaerentibus.

Plants 6·5–11·5 cm. long, main axis distinct, simple, up to 1265μ wide, wall 30μ thick, densely clothed by rhizoidal outgrowths from bases of main branches; principal branches 410–450μ wide, wall 7·5μ thick, constricted at base; both orders of branches arranged radially; ramuli bare below but clothed above with numerous pinnules radially arranged towards the base, more or less distichous above, forming a linear-lanceolate plume; pinnules 110–128μ wide; constricted at base; lowest pinnules and ramuli in a series having rhizoidal outgrowths at their bases; plants olive green in colour; main axis adhering imperfectly to paper, plumes adhering well. (Fig. 137, Pl. 41.) Type specimen in Herb. V.W.L. no. 5292, from Scott's Pt.)

Distribution. Local: 90 Mile Beach (Scott's Pt), Lyall Bay, Breaker Bay, Island Bay, Taylor's Mistake. Endemic.

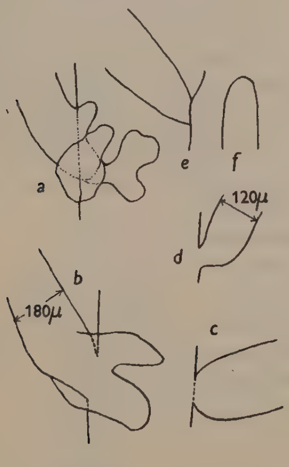

Fig. 137.

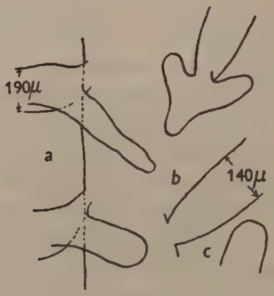

Fig. 138.

Fig. 137. *Bryopsis rhizoidea*: *a*, *b*, base of ramuli with rhizoidal outgrowths; *c*–*e*, base of upper ramuli; *f*, apex of pinnule.

Fig. 138. *Bryopsis pseudocorymbosa*: *a*, rhizoidal outgrowths; *b*, base of pinnule; *c*, apex of pinnule.

This species is closely allied to *B. corticulans* of the Pacific Coast of North America. It differs, however, in that the rhizoids are more numerous and are found in the pinnules as well as in the ramuli (latter only in *B. corticulans*). Further, both radial and distichous branching occur, whereas branching is wholly radial in *B. corticulans*. During the winter months the pinnules appear somewhat shorter.

(5) **Bryopsis pseudocorymbosa** sp.nov.

Plantis ad 7·5 cm. longis, axe primario non conspicue distincto, simplici vel fastigiate ramoso, 280–375μ lato, pariete 7·5μ crasso; ramis primariis radialiter dispositis, sed in gregibus interruptis corymbosæ orientibus, 188–200μ latis, interdum surculis rhizoidalibus e basi constricta orientibus; parte superiore ramorum armata pinnulis brevibus radialiter dispositis, 130–150μ latis, basi constrictis, apice obtuso-rotundatis, hieme caducis; pinnulis plumam lineari lanceolatam formantibus; plantis colore oleagino, ad chartam sat bene adhaerentibus.

Plants up to 7·5 cm. long, main axis not markedly distinct, simple or branched in a fastigiate manner, 280–375μ wide, wall 7·5μ thick; main branches radially arranged but arising in interrupted groups in a corymbose fashion, 188–200μ wide, some having rhizoidal outgrowths from their constricted base; the upper portion of the branches beset with short, radially arranged pinnules 130–150μ wide, constricted at the base and obtusely rounded at the apex, deciduous in the winter; pinnules forming a linear lanceolate plume; plants olive green in colour, adhering fairly well to paper. (Fig. 138; Pl. 42.) Type specimen, P.R.B. no. 69,208 from Lyall Bay.

Distribution. Local: Lyall Bay (in rock pools), Seatoun, Lyttelton, Piha. Endemic.

This species is characterized by the nature of the branching, the extremely deciduous nature of the pinnules and the rhizoidal outgrowths at the base of the major ramuli. In this respect it is like the preceding species but the pinnules are much broader.

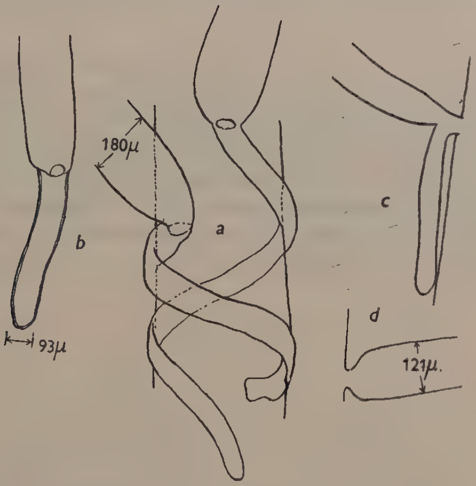

Fig. 139. *Bryopsis scarfei*: *a–c*, bases of ramulii *d*, base of pinnule.

(6) **Bryopsis scarfei** sp.nov.

Plantis ad 7·5 cm. longis, axe primario non distincto; axe 525μ lato prope basim, pariete 7·5μ crasso, 236–290μ lato prope apicem, pariete 3·75μ crasso; axe vestito ramulis gracilibus, elongatis, radialiter dispositis, ipsis ramulis vestitis pinnulis multis gracilibus brevibus 111–160μ latis, radialiter dispositis et interrupte orientibus; pinnulis basi constrictis, hieme caducis, ramulis 180–190μ latis, basi constrictis; ramulis inferioribus praeditis rhizoidibus singulis longis 73–93μ latis deorsum crescentibus, interdum circum axem modo spirae tortis; planta colore gramino-viridi; ad chartam bene adhaerente.

Plants up to 7·5 cm. long with an indistinct main axis; axis 525μ wide near base, wall 7·5μ thick, 236–290μ wide near apex, wall 3·75μ thick; axis clothed with slender, elongate ramuli arranged radially, the ramuli themselves clothed with numerous slender, short pinnules 111–160μ wide arranged radially and arising in an interrupted manner; pinnules constricted at the base, becoming deciduous in winter; ramuli 180–190μ wide, constricted at the base, the lower ramuli each with a single, long, down-growing rhizoid, 73–93μ wide, which may twine spirally around the axis; plant grass green, adhering well to paper. (Fig. 139, Pl. 42.) Type specimen, P.R.B. no. 69,207 from Lyall Bay.

Distribution. Local: Lyall Bay in a pool of discoloured water near H.W.M.; Island Bay? Endemic.

This species was recognized as probably being new to science by Mr Scarfe and it gives me much pleasure to name the species after him. It is characterized by the delicate nature of the plant as a whole, the deciduous character of the pinnules, the single, long, down-growing rhizoid from the lower ramuli and the apparent lack of a distinct main axis when the plant is laid out on a herbarium sheet. It is definitely distinct in habit from the other species with rhizoidal outgrowths, e.g. *B. rhizoidea*, and *B. pseudocorymbosa*. It appears to be very close to *B. corticulans* of the U.S.A. but differs from that species in habit and also in the greater thickness of the pinnules.

(7) **Bryopsis moorei** sp.nov.

Plantis ad 15 cm. altis, praeditis axe singulo non ramoso ad 1·6 mm. diametro prope basim, 900μ supra, pariete 30μ crasso, conspicue lamellato; axe infra nudo, superne vestito ramulis multis radialiter dispositis, 637μ latis infra, pariete 9μ crasso, decrescentibus ad 337μ prope apicem; ramulis basi constrictis, infra nudis, sed prope apicem ferentibus cristam brevem pinnularum radialiter dispositarum, 150–225μ latarum, basi constrictarum, apice ramulorum ultra pinnulas eminente; planta tota est figura lineari, colore oleagino, axe primario non bene, parte plumosa bene, ad chartam adhaerentibus.

Plants up to 15 cm. high with a single unbranched axis up to 1·6 mm. dia. near the base, 900μ higher up, wall 30μ thick, distinctly lamellate; axis bare below but clothed above with numerous radially arranged ramuli 637μ wide below, decreasing to 337μ near the apex; wall 9μ thick near base; ramuli constricted at the base, bare below but bearing towards the apex a short tuft of radially arranged pinnules 150–225μ wide, constricted at the base, the apex of the ramuli projecting beyond the pinnules; the entire plant linear in outline; olive green in colour; main axis not adhering well to paper, plumular portion adhering well. (Fig. 140. Pl. 43.) Type specimen, P.R.B. no. 47,446 from Cape Kidnappers.

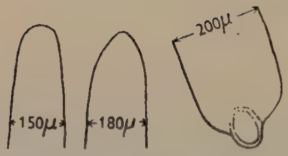

Fig. 140. *Bryopsis moorei.*

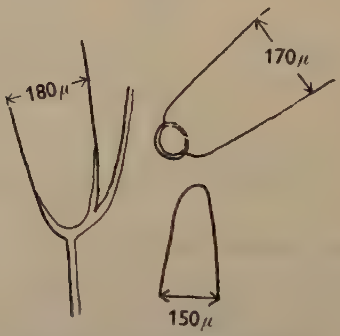

Fig. 141. *Bryopsis lindaueri.*

Distribution. Local: Ocean Beach (Cape Kidnappers) on rocks in sand. Endemic.

It gives me great pleasure to name this remarkable species after Miss L. B. Moore who first found it. In general appearance it is not unlike a very lax form of *B. vestita* f. *laxa* but is lighter in colour and the ramuli and pinnules are broader; furthermore, the pinnules are restricted to the apical region of the ramuli. There is a ring of thickened material at the base of the pinnules which is very pronounced. It is also closely allied to *B. australis* Sond. but it differs from that species in the radial arrangement of the primary ramuli (distichous in *B. australis*) and in their greater length.

(8) **Bryopsis lindaueri** sp.nov.

Plantis 4–6·5 cm. longis, axe primario distincto, plerumque simplici, vestito ramulis ita prope basim longioribus ut frons tota corymbosae similis videatur; ramulis radialiter dispositis, basi 375–525μ latis, pariete 7·5–9·2μ crasso, 262–317μ latis prope apicem, pariete 4·6–7·4μ crasso; ramulis prope apicem armatis pinnulis multis radialiter dispositis, inferioribus longioribus quam superioribus; pinnulis 150–188μ latis, basi constrictis, aestate caducis; planta ad chartam sat bene adhaerente, colore oleagino.

Plants 4–6·5 cm. long, main axis distinct, usually simple, clothed with ramuli that are longer towards the base so that the whole frond has a corymbose appearance; ramuli radially arranged, 375–525μ wide at the base, wall 7·5–9·2μ thick, 262–317μ wide near the apex, wall 4·6–7·4μ thick; ramuli beset towards the apex with numerous radially arranged pinnules, the lower longer than the upper; pinnules 150–188μ wide, constricted at the base, deciduous in summer; plant olive green in colour; adheres moderately well to paper. (Fig. 141, Pl. 43.) Type specimen in herb. V.W.L. no. 2257, from Reef Pt.

Distribution. Local: Reef Pt (pool), Lyall Bay (drift), Moa Pt (upper pools). Endemic.

This species is characterized by the nature of the branching. It appears to be somewhat variable in form and should be cultured. I have much pleasure in naming this species after Mr Lindauer who discovered it.

(9) **Bryopsis canterburyensis** sp.nov.

Plantis 7–17 cm. longis, axe primario 840–850μ lato, pariete 18μ crasso, distincto, simplici vel ramis raris; ramis 487μ dia., pariete 7·5μ crasso; axe primario, excepto valde immaturo, infra nudo, superne vestito ramis pinnatim vel irregulariter dispositis; ramis infra nudis, superne vestitis vel pinnis distichosis dispositis, 243–412μ dia., vel pinnulis simplicibus, 110–150μ latis, hieme caducis; ramis, pinnis, pinnulis basi modice constrictis, pinnulis superioribus minus conspicue constrictis; plantis bene ad chartam adhaerentibus, colore oleagino.

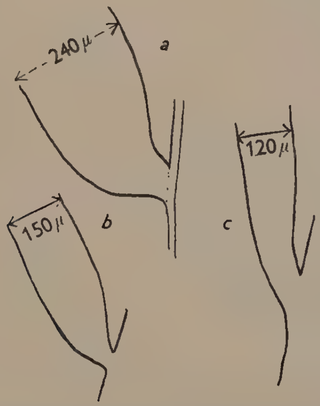

Fig. 142. *Bryopsis canterburyensis*: bases of pinnae and pinnules of different sizes.

Plants 7–17 cm. long, main axis 840–850μ wide, wall 18μ thick, distinct, simple or with occasional branches; branches 487μ dia., wall 7·5μ thick; main axis naked below except when very young, clothed with pinnately or irregularly arranged branches above; branches bare below, clothed above with distichously arranged pinnae 243–412μ dia., or simple pinnules 110–150μ wide, deciduous in winter; branches, pinnae and pinnules slightly constricted at the base, upper pinnules less distinctly constricted; plants olive green in colour; adhering well to paper. (Fig. 142, Pl. 44.) Type specimen in Laing Herbarium from Lyttelton.

Distribution. Local: Barge (Wellington Harbour), Island Bay, Lyall Bay, Lyttelton piles, Gladstone Pier. Endemic.

This species is characterized by its large size and very coarse character.

(10) **Bryopsis derbesioides** sp.nov.

Planta 3 cm. longa, nullo conspicuo axe primario, axibus 150–205μ dia. prope basim, pariete 2–3μ crasso, 111–130μ crassis prope apicem, ramulis sparsis, elongatis, irregulariter orientibus, radialiter ramosis, pinnulis 48–53μ diametro, basi vix constrictis; planta colore fusco-oleagino, ad chartam bene adhaerente.

Plant 3 cm. long, no obvious main axis, axes 150–205μ dia. near base, wall 2–3μ thick, 111–130μ thick near the apex, with sparse elongate ramuli arising irregularly, branching radial, pinnules 48–53μ dia., scarcely constricted at the base; plant dark olive green; adhering well to paper. (Fig. 143, Pl. 45.) Type specimen V.W.L. 106 in herb. Auck. Inst., remainder co-types.

Distribution. Local: Moto Arohia. Endemic.

This species is fine and feathery and is closely allied to *B. hypnoides*. It differs from that species in the smaller size of the pinnules, the absence of a main axis, and less profuse branching. It has, in fact, the general habit of a large *Derbesia* as seen with the naked eye. It is also allied to *B. otagensis* but it differs in the smaller size and in the absence of a main axis.

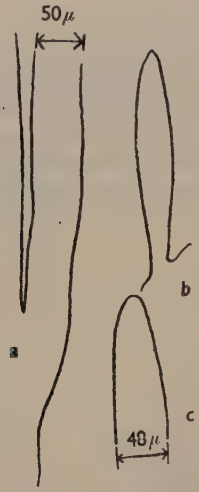

Fig. 143. *Bryopsis derbesioides*: *a*, base of pinna; *b*, pinnule; *c*, apex of pinna.

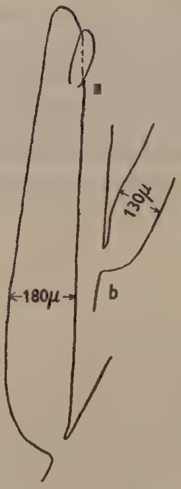

Fig. 144. *Bryopsis olivacea*.

(11) **Bryopsis olivacea** sp.nov.

Plantis 4·5–7·5 cm. longis, axe primario distincto, plerumque simplici, 360–467 μ dia., pariete 8–14μ crasso, vestito ramis distichosæ dispositis, 225–287μ longis, pariete 4–5μ crasso, basi constrictis, ramis infra nudis, vestitis prope apicem pinnulis distichosæ dispositis, 121–188μ latis, basi constrictis, deinde caducis, paulatim ad apicem arctioribus, interdum ramulis brevibus prope apicem accedentibus; plantis colore oleagino, ad chartam bene adhaerentibus.

Plants 4·5–7·5 cm. long, main axis distinct, usually simple, 360–467μ dia., wall 8–14μ thick, clothed with distichously arranged branches 225–287μ long, wall 4–5μ thick, constricted at the base, branches bare below, clothed towards the apex with distichously arranged pinnules 121–188μ wide, constricted at the base, deciduous later, tapering gradually to the apex, some with short subsidiary branchlets near the apex; plants olive green in colour, adhering well to paper. (Fig. 144; Pl. 45.) Type in Laing Herbarium, from Akaroa.

Distribution. Local: Seatoun, Evans Bay, Lyall Bay, Akaroa, Portobello. Endemic.

The summer form of this species has more numerous pinnules and looks slightly different in appearance. The species differs from *B. canterburyensis*, which it resembles in many respects, by its smaller size and more densely set pinnules. It differs from *B. plumosa*, which it resembles in habit, by the greater size of the pinnules and pinnae.

(12) **Bryopsis tetrasticha** sp.nov.

Plantis 3–8 cm. longis, axe primario distincto, simplici vel ramoso, 412μ plusve lato, pariete 13μ crasso; axe et ramis armatis ramulis plerumque in 4 ordines, binos ab utroque latere, interdum radialiter dispositis, 272–318μ latis, ramulis tetrastichosa armatis pinnulis 75–138μ latis, dispositione tetrastichosa in radialem mutata ad ipsum apicem, ubi color valde densus est; planta tota aspectu plumoso, colore fusco-oleagino, ad chartam bene adhaerente.

Plants 3–8 cm. long, main axis distinct, simple or branched, 412μ wide or more, wall 13μ thick; axis and branches beset with ramuli usually arranged in 4 rows, two each side, sometimes radially, 272–318μ wide, the ramuli beset in a tetrastichous fashion with pinnules 75–138μ wide, the tetrastichous arrangement becoming radial towards the very apex where the colouring is very dense; the entire plant feathery in appearance, deep olive green, adhering well to paper. (Fig. 145; Pl. 45.) Type specimen in Laing Herbarium from Akaroa.

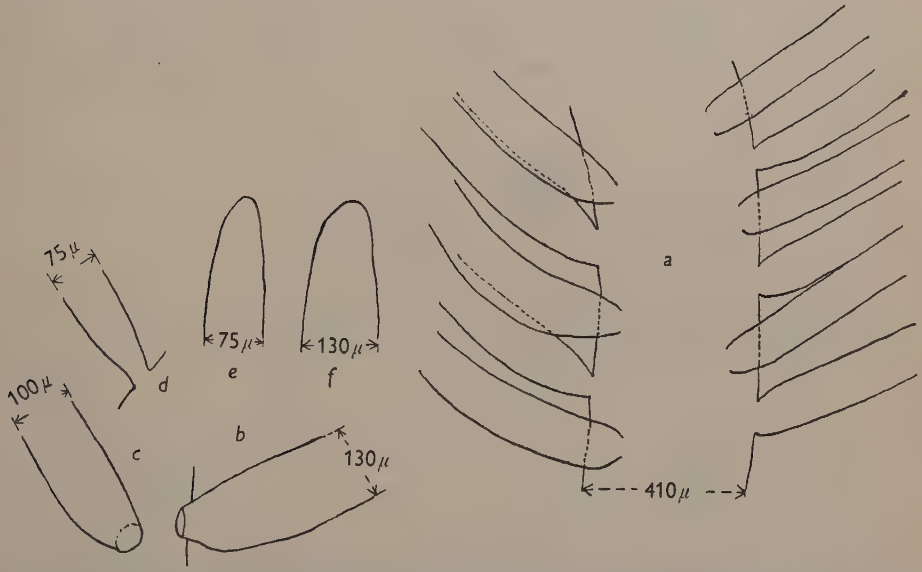

Fig. 145. *Bryopsis tetrasticha*: *a*, part of thallus showing pinna arrangement; *b–d*, base of pinnules; *e*, *f*, apex of apical and basal pinnule respectively.

DISTRIBUTION. Local: Houghton Bay, Lyall Bay, Worser Bay, Akaroa, Lyttelton Harbour, Diamond Harbour. Endemic.

In appearance this species is very like *B. hypnoides* but it differs from it in the typical tetrastichy, and also in the larger size of the pinnules and pinnae.

(13) *Bryopsis duchassaingii* J. Ag.

Collins, Green Alg. N. Amer. p. 323, 1909.

Plant 2–20 cm., main axis simple or sparsely branched, 412–862μ wide, wall 9–18μ thick, clothed towards the apex with a dense mass of short stout pinnules, almost distichous below, radially arranged above, 150–290μ dia., constricted at the base, deciduous below, straight or slightly incurved, the lower pinnules sometimes with a rhizoidal outgrowth at the base; plant dark green, adheres well to paper. (Fig. 146.)

DISTRIBUTION. Local: Little Barrier, Cape Turnagain (?) (on *Halopteris*), Ohiro Bay, Moa Pt., Houghton Bay, Titahi Bay, Lyall Bay. General: West Indies, Florida.

There may be two species or varieties here and further collections are desirable.

(14) *Bryopsis pennatula* J. Ag.

J. Ag., *Till Alg. Syst.* 5, 23, 1886 (as *B. pennata β minor*); Kütz., *Tab. Phyc.* 6, tab. 76, II, 1856.

Plant 2–4 cm. tall, main axis distinct, simple or occasionally branched, 450–490μ dia., wall 11μ thick and clothed towards the apex with closely set distichous pinnules 150–188μ near the base, becoming finer near the apex, 80–100μ, constricted at the base; plants olive green in colour, adhering well to paper. (Fig. 147.)

Distribution. Local: on *Halopteris*, Reef Pt, Tunnel Beach. General: West Indies, Mexico, Ceylon.

This specimen has been checked with authentic material from Mexico kindly lent by the University of California.

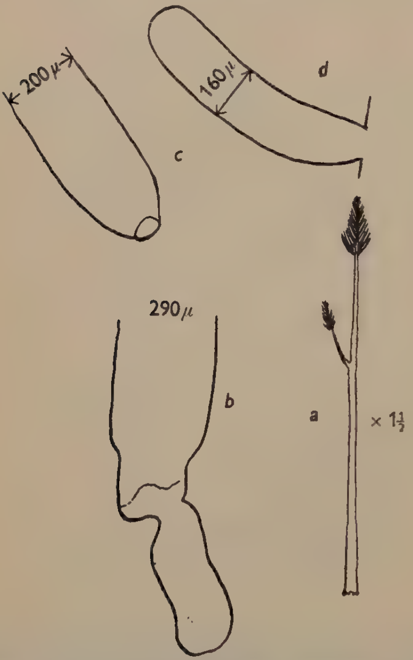

Fig. 146. *Bryopsis duchassaingii*: *a*, plant; *b*, base of lower pinnule; *c*, *d*, upper pinnules.

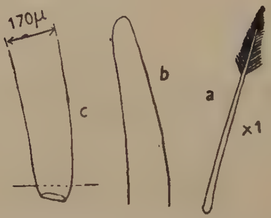

Fig. 147. *Bryopsis pennatula*: *a*, plant; *b*, apex of pinnule; *c*, base of pinnule.

(15) **Bryopsis pseudoplumosa** sp.nov.

Planta ad 4 cm. longa, axe primario distincto, armato ramis multis radialiter dispositis, 216–412μ dia., pariete 7·5μ crasso, vestito prope basim pinnulis radialiter dispositis, prope apicem distichosæ dispositis, 111–150μ dia., basi constrictis; planta colore fusco-oleagino, ad chartam bene adhaerente.

Plant up to 4 cm. long, main axis distinct, beset with numerous radially arranged branches 262–412μ dia., wall 7·5μ thick, clothed towards the base with radially arranged pinnules, distichously arranged towards the apex, 111–150μ dia., constricted at the base; plant deep olive green; adheres well to paper. (Fig. 148, II; Pl. 45.) Type specimen in Laing Herbarium, from Taylor's Mistake.

Distribution. Local: Taylor's Mistake. Endemic.

This species is very similar in habit to *B. plumosa*, but differs from it in the larger size of the pinnules and the lower radial arrangement. It is not unlike *B. rhizoidea* in some of the measurements, but it differs distinctly in habit.

(16) **Bryopsis pseudopennata** sp.nov.

Plantis 2–4·5 cm. longis, axe primario distincto, simplici vel interdum ramoso, ubique armato ramulis distichosæ dispositis, ad 2·5 cm. longis, 318–563μ dia., pariete 7·5–11μ crasso, partibus superioribus ramulorum vestitis pinnulis dense aggregatis, 168–197μ dia., pluma figurae lineari-lanceolatae; pinnulis basi constrictis, inferioribus surculos breves rhizoidales ferentibus; planta colore oleagino, ad chartam bene adhaerente.

Plants 2–4·5 cm. long, main axis distinct, simple or occasionally branched, beset throughout with distichously arranged ramuli up to 2·5 cm. long, 318–563μ dia., wall 7·5–11μ thick, upper parts of ramuli clothed with closely set pinnules 168–197μ dia., the plume being linear-lanceolate in outline; pinnules constricted at the base, the lower with short rhizoidal outgrowths; plant olive green; adhering well to paper. (Fig. 148, I; Pl. 46.) Type specimen herb. P.R.B. no. 46,695, from Worser Bay.

Distribution. Local: Worser Bay (Wellington), Moa Pt, Lyttelton. Endemic.

This species differs from *B. pennata* in the greater length of ramuli; also the base of the ramuli are bare. The colour is olive green as against grass green and *B. pennata* is much more feathery in appearance. It also appears to be closely allied to *B. setacea* of S. Africa, but there is a difference in the shape of the frond and *B. setacea* lacks the rhizoidal outgrowths.

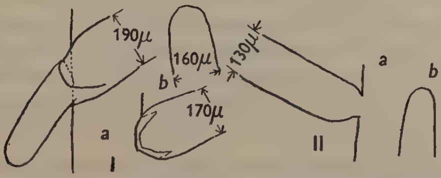

Fig. 148. I. *Bryopsis pseudopennata*: *a*, base of pinnule; *b*, apex of pinnule. II. *B. pseudoplumosa*: *a*, base of pinnule; *b*, apex of pinnule.

(17) *Bryopsis corymbosa* J. Ag.

J. Ag., *Alg. Mar. Med.* p. 21, 1842; Feldmann, Alg. Mar. Côte des Albères, *Rev. Alg.* **9**, p. 227, fig. 28, 1937.

Plant 2–3 cm. long, tufted, bushy, no distinct main axis, beset with numerous radially arranged branches 126–168 (–210)μ wide, themselves covered with radially arranged pinnules 80–110μ dia.; plant grass green; adhering well to paper. (Fig. 149, I.)

Distribution. Local: Russell, Kawhia, Lyttelton. General: Australia, Tierra del Fuego, Falklands.

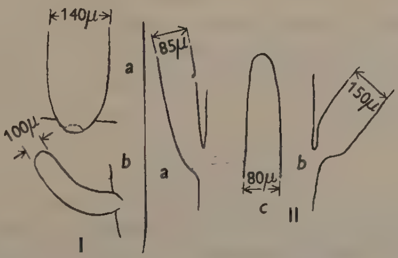

Fig. 149. I. *Bryopsis corymbosa*: *a*, base of older pinna; *b*, ultimate pinnule. II. *B. fusca*: *a*, *b*, base of pinnule and pinna respectively; *c*, apex of pinnule.

The specimen from Lyttelton in the Laing herbarium is not well preserved and is covered with sediment. It is only placed in this species tentatively. The other plants agreed closely with authentic material kindly loaned by the University of California.

(18) **Bryopsis fusca** sp.nov.

Plantis 2–2·5 cm. longis, nullo conspicuo axe primario, thallo toto cristato, ramulis 150–300μ dia., pariete 4–11μ crasso, parietibus crassioribus conspicue lamellatis, ramulis armatis pinnulis elongatis, radialiter dispositis, 75–100μ dia., inferioribus basi presse constrictis, superioribus attenuatis; planta tota aspectu delicato, colore fusco-viridi, ad chartam bene adhaerente.

Plants 2–2·5 cm. long, no distinct main axis, whole thallus tufted, ramuli 150–300μ dia., wall 4–11μ thick, the thicker walls being distinctly lamellate; ramuli beset with radially arranged elongate pinnules 75–100μ dia., lower ones sharply constricted at the base, upper attenuate; whole plant delicate in appearance, deep dark green in colour; adheres well to paper. (Fig. 149, II; Pl. 46.) Type specimen in herb. P.R.B. no. 38,026, from Matauri Bay.

DISTRIBUTION. Local: Matauri Bay (drift), Nelson. Endemic.

This is a very slender delicate form, very compact and tufted and therefore differing from *B. otagensis*. The only other species with this habit is *B. tetrasticha*.

(19) *Bryopsis corticulans* Setch. var. **novaezelandiae** var.nov.

Plantis ad 2 cm. altis, axe primario simplici vel perraro ramoso, 543–637μ dia., pariete 18–20μ crasso, armato ramulis radialiter dispositis, 200–230μ dia., pariete 4μ crasso, basi constrictis, surculos rhizoidales e basi axem primarium corticulantes ferentibus; parte superiore ramulorum armata pinnulis radialiter dispositis, paulum incurvatis, basi constrictis, inferioribus armatis brevibus vel incipientibus rhizoidibus; pinnulis 65–87μ dia.; planta colore gramino-viridi, ad chartam bene adhaerente.

Plants up to 2 cm. tall, main axis simple or very occasionally branched, 543–637μ dia., wall 18–20μ thick, beset with radially arranged ramuli 200–230μ dia., wall 4μ thick, constricted at the base and with rhizoidal outgrowths from the base corticating the main axis; ramuli beset in their upper part with radially arranged pinnules, slightly incurved, constricted at the base, the lower ones with short or incipient rhizoids; pinnules 65–87μ dia.; plant grass green; adheres well to paper. (Fig. 150; Pl. 46.) Type specimen in herb. Auck. Inst., from Takapuna.

DISTRIBUTION. Local: pool at H.W.M. Takapuna, Port Fitzroy, Shag Rock, Raukura Pt, Fletcher's Bay, Pihama. Endemic.

This variety is close to *B. corticulans* Setch., but differs from it in its smaller size and greater development of rhizoids. It differs from *B. rhizoidea* also in its smaller size and in the fact that the arrangement is clearly radial throughout.

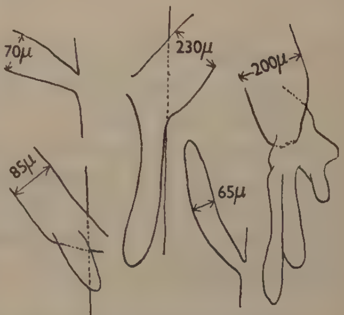

Fig. 150. *Bryopsis corticulans* var. *novaezelandiae*.

CODIACEAE

Thallus dark green, spongy, subspherical, applanate or erect, cylindrical, flattened or jointed, simple or more or less dichotomously branched, at times lime encrusted, composed of intertwined branching filaments, the peripheral branchlets forming a palisade or pavement-like external layer; septa frequent but only formed in connexion with formation of reproductive organs or in older filaments; chloroplasts parietal, small, numerous, especially in apices; pyrenoids absent; multiplication by fragmentation, zoospores and anisogametes.

Codium Stackhouse

Thallus spongy, dark green, consisting of a much-branched, tubular, coenocytic cell, with branches compacted to form a plant body of definite shape applanate, globose or cylindrical, simple or dichotomously branched, not encrusted with lime; external layer composed of a compact palisade of swollen branch-tips (the 'utricles'), arising from an internal layer of colourless, medullary filaments, loosely or densely intertwined; chloroplasts small, disk-shaped, without pyrenoids, densely aggregated in tips of utricles: homo- or heterothallic; reproduction by biflagellated anisogametes produced in gametangia which are situated laterally, one or two per utricle.

The treatment of this genus is the work of Miss U. V. Dellow. In revising the genus it has been necessary to study much material both from New Zealand and overseas. A more detailed account has appeared separately (Dellow, 1952).

1.	Thallus prostrate.	2
	Thallus erect.	4
2.	Utricles cylindrical, 400–900μ long.	3
	Utricles large, 4–6 mm. long.	*C. cranwelliae*
3.	Membrane thin, often constricted below apex of utricle.	*C. adhaerens* var. *convolutum*
	Membrane thickened, apex of utricle narrower than base.	*C. adhaerens* var. *incrassatum*
4.	Branching sparingly dichotomous, utricles never mucronate.	*C. cuneatum* f. *striatissimum*
	Branching profusely dichotomous, utricles mucronate or not.	5
5.	Branches slender, utricles 300–570μ long.	*C. gracile*
	Branches coarser, utricles 700–1500μ long.	6
6.	Utricles with a more or less prominent mucro.	*C. fragile*
	Utricles never mucronate.	*C. dichotomum f. novo zelandicum*

(1) *Codium adhaerens* (Cabr.) Ag. var. *convolutum* Dellow

J. Ag., De Alg. Nov. Zel. Mar. p. 3, 1877; Harv. in Hooker, *Fl. Nov. Zel.* **2**, 261, 1855; *Handb. N.Z. Fl.* p. 714, 1867 (all as *C. adhaerens*, *pro parte*); Dellow, *Trans. Roy. Soc. N.Z.* **80**, 122, 1952.

Thallus dark green, prostrate, adhering closely to substratum when young, becoming loosely attached or free when old, with few to many irregular radial lobes and corrugations, up to 20 cm. in diameter and 2 cm. thick; outer surface firm, slippery to touch; external layer of palisade-like, densely packed, branched utricles, 420–900μ long, sometimes as much as 1280μ long, 28–100μ, rarely 200μ, wide; plastids aggregated near apices of utricles; apex varying greatly in shape from swollen and rounded with a constriction below to flat or slightly depressed; hairs or scars forming a ring round subapical region; hairs up to twice the length of utricles, 41–132μ long and 15–30μ wide; apex flat or rounded; plastids scattered throughout; subsurface layer of clavate utricles with thin membranes and few plastids, up to 1400μ long and 170μ wide; medullary filaments 15–75μ dia.; heterothallic; gametangia pedicellate, one per utricle, fusiform, attached between half and one-third distance from apex of utricle, 240–400μ long and 40–140μ wide. (Fig. 151.) V.W.L. no. 252 as *C. adhaerens*, no. 794 as *C. coronatum*.

In tide pools, and on exposed rocks between E.H.L.W.N. and M.L.W.S., frequently epiphytic on *Corallina officinalis*, flourishing in sandy or muddy localities.

DISTRIBUTION. Local: north Cape to Banks Peninsula, Puketeraki; frequent. Endemic.

This variety is distinguished from *C. adhaerens* '*sensu stricto*' by the intense degree of folding and the greater robustness of mature thalli, together with the single ring of hairs and the often constricted region below the apices of the utricles. Knox (1952) considers that its distribution is determined by shade and degree of exposure to wave action.

(2) *Codium adhaerens* var. *incrassatum* Dellow

J. Ag., De Alg. Nov. Zel. Mar. p. 3, 1877; Harv. in Hooker, *Fl. Nov. Zel.* 2, 261, 1855; *Handb. N.Z. Fl.* p. 714, 1867 (all as *C. adhaerens, pro parte*); Dellow, *Trans. Roy. Soc. N.Z.* **80**, 124, 1952.

Thallus dark green, firmer than var. *convolutum*, applano-pulvinate, lobed at margins; lobes more regularly dichotomous, 1–2 cm. broad with truncated apices, separated for a considerable part of their length; utricles 900–1300μ long and 50–100μ wide, cylindrical from base up, narrowing to form an apex like a bottle neck; membrane varying from 1 to 20μ thick; thickened membranes flat or slightly depressed, often stratified and alveolate; hairs absent; clavate utricles not seen; medullary filaments 15–60μ dia.; gametangia not seen. (Fig. 151.)

DISTRIBUTION. Local: St Clair, Stewart Is. Endemic.

This variety differs from the form characteristic of more northern New Zealand waters in the firmer, less markedly lobed thallus, the bottle-shaped utricles and the presence of distinctly thickened membranes in the utricles.

(3) *Codium cranwelliae* Setch.

Setchell, *Proc. Nat. Acad. Sci.* **26** (7), 446, figs. 1–5, 1940; Dellow, *Trans. Roy. Soc. N.Z.* **80**, 125, 1952.

Thallus light greyish green, globose, spongiose, ovoid to round with one to three lobes, 0·5–5 cm. long, 0·5–3 cm. broad, erect, attached relatively loosely to substratum over a small portion of base; tips of utricles glistening, visible to naked eye; utricles 'megistophyse', 4000–6500μ long, 400–625μ wide, sparsely branched, more or less cylindrical with irregular projections from base; apex rounded or flattened, apical and subapical membrane up to 10μ thick with branched and unbranched lamellate trabeculae projecting into utricle cavity; hairs absent; plastids discoid to elongate, sometimes polygonal through mutual pressure, as much as 10μ long and 5μ wide; medullary filaments 35–70μ dia., densely intertwined; gametangia ovoid to fusiform, in patches over exposed portion of thallus, on a short pedicel, 700–780μ long and 200–300μ wide, usually one, occasionally two per utricle; in latter case development not simultaneous; attached between 1000 and 1300μ from apex, i.e. about one-quarter the total length of utricle from apex; diameter of pore 70–85μ. (Fig. 151.) V.W.L. 182.

On rocks exposed just above L.W.N.T. mark down to below E.L.W.S.

DISTRIBUTION. Local: Tarpeka Pt (Bay of Islands), Poor Knight Is., Oruawharo Bay. Endemic.

(4) *Codium fragile* (Sur.) Hariot var. *typicum* O. C. Schmidt

O. C. Schmidt, Beit. Kennt. Gatt. *Codium*, p. 47, figs. 29–31, 1923; J. Ag., De Alg. Nov. Zel. Mar. p. 3, 1877 (as *C. tomentosum*); Harv. in Hooker, *Fl. Nov. Zel.* **2**, 261, 1855 (as *C. tomentosum*); *Handb. N.Z. Flora*, p. 714, 1867 (as *C. tomentosum*); De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 92, 1923 (including *C. muelleri* as *C. tomentosum*); Reinbold, Ergeb. reis. nach dem Pacif., p. 288, 1899 (as *C. mucronatum*); Dellow, *Trans. Roy. Soc. N.Z.* **80**, 130, 1952.

Thallus erect, dark green, regularly or irregularly dichotomously branched; branches 10–25 cm. tall and 2–10 mm. dia., terete, broader and sometimes slightly flattened below a major dichotomy, arising from a small, unevenly lobed, prostrate holdfast 1–3 cm. dia.; surface of branches often covered with a dense tomentum of hairs; utricles unbranched, cylindrical or clavate to pyriform, varying in length from 750 to 1500μ, and in diameter from 30 to 350μ, usually narrower at base; apical membrane 8–40μ thick, with or without a prominent mucro; pores or stratifications occasionally present; hairs attached between one-third and one-quarter total length of utricle from apex, slightly swollen at base, rounded at apex, 150–500μ long and 25–40μ wide, plastids present; pith filaments

40–60μ dia.; heterothallic (?); gametangia 1–2 per utricle, where 2, development often not simultaneous; ovate to fusiform, attached between one-third and one-half distance from base to apex, 300–500μ long and 90–120μ wide. (Fig. 151.)

Growing in pools and on rocks exposed at M.L.W.N.T.

Distribution. Local: east coast of all Islands, Hokianga, Pt Nicholson, Lyall's Bay,

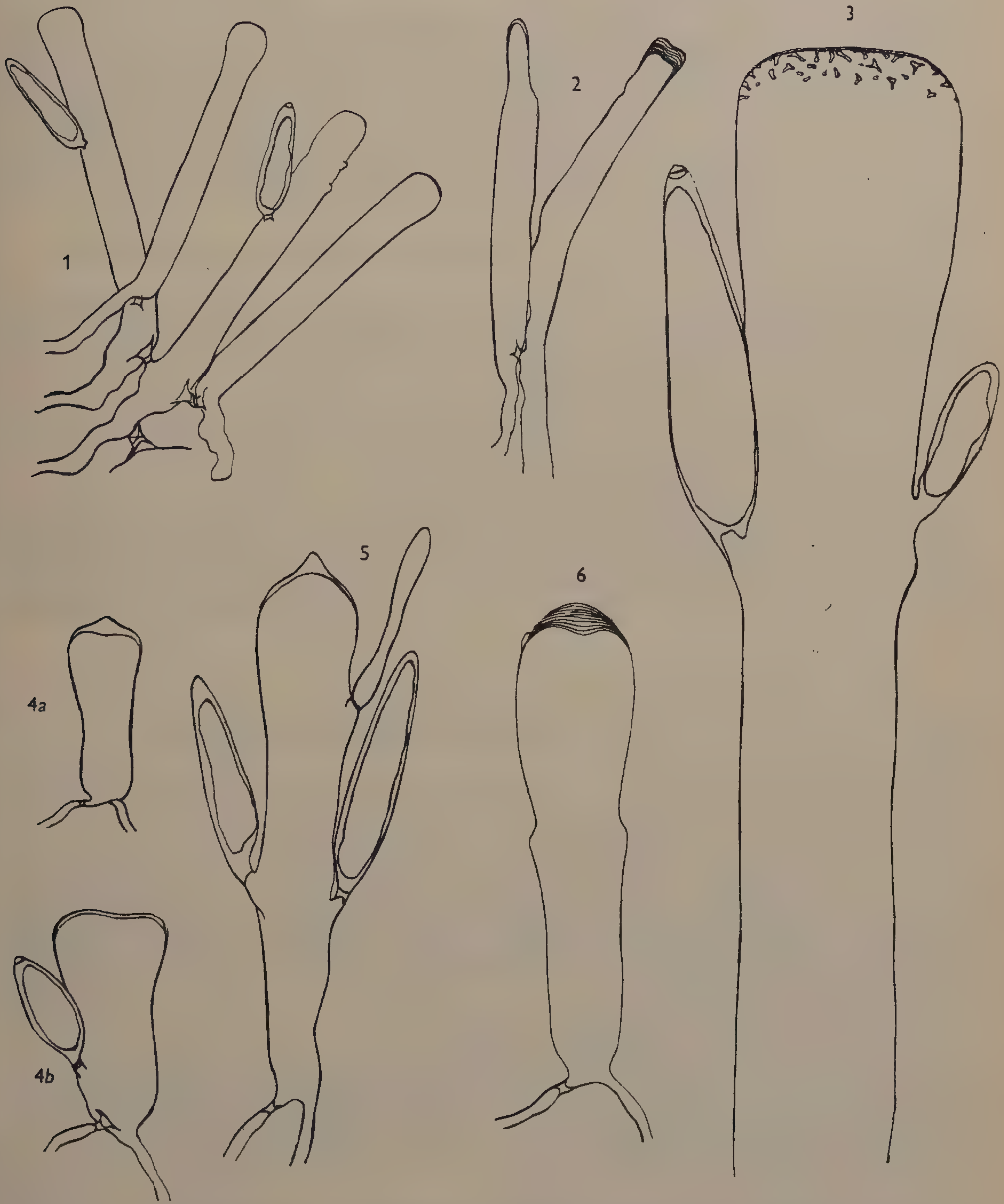

Fig. 151. 1, *Codium adhaerens* var. *convolutum*: utricles with gametangia; 2, *C. adhaerens* var. *incrassatum*: utricles; 3, *C. cranwelliae*: trabeculate 'megistophyse' utricle with unequal development of gametangia; 4*a*, *C. gracile*: sterile utricle; 4*b*, *C. gracile*: fertile utricle; 5, *C. fragile*: utricle with immature male gametangia; 6, *C. cuneatum* f. *striatissimum*: utricle. (All ×50.) (U. V. Dellow del.)

Port Chalmers, Portobello, Chatham Is., Subantarctic Islands. General: Atlantic Ocean, Denmark, Netherlands, Ireland, S. Africa, Tierra del Fuego, Indian Ocean, Cape of Good Hope, Natal, Kerguelen, Australia, Pacific Islands, California to Alaska.

(5) *Codium gracile* (O. C. Schmidt) Dellow

O. C. Schmidt, Beit. Kennt. Gatt. *Codium*, **48**, fig. 32, 1923 (as *C. fragile* var. *gracile*); Dellow, *Trans. Roy. Soc. N.Z.* **80**, 135, 1952.

Thallus erect, regularly dichotomously branched, dark green, up to 45 cm. long, 1–4 mm. dia., terete, solid; holdfast slightly irregular in outline; utricles small, clavate or pyriform, 300–570μ long, 64–230μ broad near apex, 40–100μ broad near base; apex varying from widely blunt and slightly depressed to narrow and sharply mucronate; membrane 6·0–55·0μ thick; hairs and hair scars absent; plugs at base of utricles 16–20μ dia.; central filaments 20–32μ dia.; gametangia 1–2 per utricle, attached about two-thirds of total distance from apex, 170–270μ long, 50–100μ broad, pedicellate; pores 20–30μ dia. (Fig. 151.) V.W.L. 784.

DISTRIBUTION. Local: Bay of Islands, Buffalo Beach, Mercury Bay, Breaker Bay, Lyall Bay. Endemic.

Distinguished from *C. fragile* (Sur.) Hariot macroscopically by the smaller diameter of the mature 'branches', and microscopically by the much smaller size of utricles and gametangia, together with the absence of hairs.

It is possible that the absence of hairs may be an ecological response to a deep water habitat (cf. absence of epiphytes on specimens), following the suggestion by Berthold (p. 420, 1882, ref. in Schmidt, p. 7, 1923) that the hairs on *Codium* utricles provide protection against too great light intensity.

Utricles from the holdfast are generally narrower and with a much more prominent mucro than those from other parts of the thallus. Pores may be found in utricles where there is a well-developed mucro. There appears to be an inverse relationship between utricle size and membrane thickness, the larger the utricle the thinner the membrane, and vice versa.

(6) *Codium cuneatum* Setch. & Gardn. f. *striatissimum* Dellow

Setchell & Gardner, *Proc. Calif. Acad. Sci.* **12** (29), 708, 1924; Dellow, *Trans. Roy. Soc. N.Z.* **80**, 137, 1952.

Mature plants erect, flabellate, as a rule regularly dichotomously branched, forked near base, up to 10 cm. long, branches coarse, wedge-shaped between forkings, up to 3 cm. broad just beneath a major dichotomy; terminal branches very short, sometimes almost pointed at apices; thallus attached by a small disk-like holdfast; utricles unbranched, 730–1400μ long, 100–300μ wide, rounded at apex, never mucronate; membrane varying greatly in thickness from 6 to 70μ, thickened membranes striated, occasionally foveolate on inner surface; utricles rarely double headed; gametangia not seen. (Fig. 151.) V.W.L. 373.

DISTRIBUTION. Local: Matauhi Bay. Endemic.

The New Zealand form differs from *C. cuneatum* f. *typicum* in possessing very much thickened, striated membranes, and in having utricle apices often narrower than the main body of the utricle. The type species and other variants are found in the Gulf of California, Java and Lord Howe Is.

(7) *Codium dichotomum* (Huds.) S. F. Gray. f. *novozelandicum* Dellow

Harv. in Hooker, *Fl. Nov. Zel.* **2**, 261, 1855; *Handb. N.Z. Flora*, p. 714, 1867; De Toni & Forti, Alg. Aust. Tasm. e Nuov. Zel. p. 92, 1923 (all as *C. tomentosum*); Dellow, *Trans. Roy. Soc. N.Z.* 80, p. 128, pl. 33, fig. 1, 1952.

Thallus erect, cylindrical, up to 18 cm. long, regularly dichotomously branched; main branches 1–3 cm. between forks, slender or somewhat thickened, 1–5 mm. dia.; utricles larger than in the species, 700–1100μ (av. 870μ) long, 140–240μ (rarely to 410μ) wide at apex, 70–100μ wide at base, apices rounded or bluntly acuminate; membrane 7–15μ thick, smooth, without grooves, occasionally perforated with a pore; hair scars occasionally present; central filaments 30–70μ dia; gametangia larger than in the species, cylindrical fusiform, 300–420$\mu \times$ 80–150μ, sometimes swollen below, attached at or just below middle of utricle, 1–4 per utricle.

DISTRIBUTION. Lyall Bay, Evans Bay, Petone, Picton, Nelson, Lyttelton, Portobello, Kermadec Is. and probably elsewhere. Endemic. (The parent species is widely distributed).

Dellow (1952) points out that the larger size of utricles and gametangia, the lack of vegetative propagules and the absence of grooves from the thickened membrane justify regarding the New Zealand material as representing a new form.

CAULERPACEAE

Plants small to large, coenocytic, multinucleate and non-septate. Whole of thallus strengthened internally by ramifying cellulose trabeculae; multiplication by fragmentation; reproduction involving local segmentation of the protoplast and discharge of gametes through papillae on the plant surface.

Caulerpa Lamouroux

Thallus with a prostrate rhizome attached to the surface by rhizoids, giving rise at intervals to erect, aerial branches varying much in form from simple foliose to pinnately branched.

1.	Rhizome covered with scales.	2
	Rhizome not covered with scales.	3
2.	Branches simple or dichotomously branched.	*C. brownii* var. *selaginoides*
	Branches pinnate.	*C. hypnoides* var. *flexilis* f. *novaezzlandiae*
3.	Axis articulate, branchlets opposite, distichous.	*C. articulata*
	Axis not articulate, branchlets distichous or imbricate.	4
4.	Ramuli sessile, spherical.	*C. sedoides* var. *novaezelandiae*
	Ramuli pedicellate, pyriform.	*C. racemosa* var. *uvifera*

(1) *Caulerpa brownii* Endl.

Rhizome stout to slender, shaggy, clothed with simple, imbricate, mucronate scales; erect fronds, cylindrical, linear or clavate, simple or sparingly branched, up to 45 cm. high but usually much shorter, beset throughout their length by numerous adpressed imbricate pinnules, irregularly arranged or verticillate towards the apex, simple or bifurcate, 4–6 mm. long, tapering at the apex into an abrupt mucro Australasia.

Caulerpa brownii var. *selaginoides* J. Ag.

J. Ag., *Till Alg. Syst.* **1**, p. 28, 1872; Weber van Bosse, Mon. des Caulerp. p. 306, pl. 25, fig. 3, 1898; Harv. in Hooker, *Fl. Nov. Zel.* **2**, 260, tab. 121 (as *C. brownii* and as *C. furcifolia*), 1855; Hook. *Handb. N.Z. Flora*, p. 713, 1867; Laing, *Trans. N.Z. Inst.* **57**, 132, 1926.

Erect fronds up to 19 cm. high, pinnules patent, spread out, not so densely arranged as in the species, the distances between branchlet origins being up to twice the diameter of a branchlet; olive to dark green, apices often yellowish green; not adhering to paper. (Pl. 47.) V.W.L. 153.

DISTRIBUTION. Local: Cape Turnagain, Lyall Bay, St Clair, Puketeraki, east coast of South Island, Banks Peninsula, Brighton (Otago), Black Hd, Bluff, Chalky Inlet, Chatham Is., Stewart Is. Endemic.

Madame Weber van Bosse gives the greatest length of this form as 8 cm. but this may be from lack of adequate material. The New Zealand plants are frequently larger than this.

Caulerpa brownii f. **laxa** form.nov.

Axe gracili, ramis apertioribus, patentibus vel adpressis, fronde erecta tota multo tenuiore.

Erect frond up to 23 cm. tall, axis slender, branchlets more open, patent or adpressed, whole frond appearing much thinner. (Pl. 48.) Type specimen in herb. Laing, from Lyall Bay.

DISTRIBUTION. Local: Lyall Bay, Island Bay, Bluff, Green Is. Endemic.

Agardh (1872) states that he found it impossible to separate the New Zealand form from the Australian. There is no doubt that the two are distinct, the New Zealand variety having a more open appearance due to the spreading nature of the branchlets. The new form *laxa* is very distinct from the typical var. *selaginoides*, but gradations can be found and there appears to be no reason for establishing a new variety. Although Hooker records the parent species from New Zealand, for the reasons stated above it is removed from the present list.

(2) *Caulerpa hypnoides* (R.Br.) Ag.

Harv., *Phyc. Aust.*, tab. 84, 1858–63; Kütz., *Tab. Phyc.* 7, tab. 18, 1857; Harv. in Hooker, *Fl. Nov. Zel.* 2, 260, 1855; *Handb. N.Z. Flora*, p. 716, 1867; Cotton, *Kew Bull. Misc. Inf.* p. 326, 1912; Laing, *Trans. N.Z. Inst.* 57, 132, 1926.

Erect fronds 20–30 cm. long, arising from a rhizomatous basal portion densely covered with cylindrical furcate scales; erect frond usually simple, stipitate and pinnately branched, branches 8–10 cm. long; trunk and branches covered with patent branchlets irregularly arranged, simple or forked, forks very patent, rather blunt, minutely bi-mucronate at the apex. General: Australasia.

Caulerpa hypnoides var. *flexilis* f. *novaezelandiae* Web. v. Bosse

Weber van Bosse, Mon. des Caulerp. p. 347, pl. 29, fig. 7, 1898.

Erect fronds up to 26 cm. long, pinnae up to 7 cm. long, main axis densely clothed with ramentae at the base but less so higher up; pinnae simple or bifurcate, clothed with patent branchlets not so densely placed as in the species; simple and furcate mixed; olive green in colour, apices of pinnae yellow-green, the whole erect system having a triangular outline. (Pl. 47.) V.W.L. 27.

This form differs from the species in the more open arrangement of the pinnae and the branchlets. The erect fronds rarely exceed 16 cm. unless the plant is growing in quiet waters.

DISTRIBUTION. Local: Houhora, Rangiputa, Bay of Islands, Little Barrier, Great Barrier, Whitianga, Cape Turnagain. Endemic.

Caulerpa hypnoides var. *flexilis* f. **antarctica** form.nov.

Frondibus erectis ad 31 cm. longis, pinnis ad 8 cm. axe et pinnis vestitis ramis, plerorumque omnibus furcatis, densius imbricatis quam in var. *novae-zelandiae*.

Erect fronds up to 31 cm. long, pinnae up to 8 cm., main axis and pinnae clothed with branchlets more densely imbricate than in var. *novae-zelandiae*, usually all furcate; dark green in colour, the outline of the erect system more linear in shape. Type specimen, P.R.B. no. 69,252, from Lyall Bay.

DISTRIBUTION. Local: Lyall Bay, Pihama. Endemic.

Specimens are available showing that this form grades into the variety. It is probable that the variety represents the northern warm-water form and f. *antarctica* the southern cold-water form. The extremes are readily separated from each other. In size and general appearance the form shows some resemblance to var. *laxa* Weber van Bosse.

(3) *Caulerpa racemosa* (Forsk.) J. Ag.

Collins, Green Alg. N. Amer., p. 419, 1909; Börg., Mar. Alg. D.W. Indies, p. 147, 1913–14; Laing, *Trans. N.Z. Inst.* 57, 132, 1926.

Plants with a branching stolon system, extending to form a patch one or more metres in diameter, erect fronds robust or delicate, simple or branched, ramuli distichous, alternate, opposite, multiseriate or imbricate; apices of ramuli rounded or plano-convex, enlarging from the base to the apex.

Caulerpa racemosa var. *uvifera* (Turn.) J. Ag. f. *intermedia* Web. v. Bosse.

Kütz., *Tab. Phyc.* **7**, tab. 14, 1857.

Erect fronds short, ramuli obovate, densely imbricate, short-stalked with a much swollen apex.

DISTRIBUTION. Local: Kermadecs. General: all tropical seas for various forms of the species.

Since only one form of *C. racemosa* occurs in New Zealand it is not possible to determine whether vars. *uvifera* and *clavifera* should be separate species. I have therefore followed Mme Weber van Bosse and Börgesen, and treated our form as a variety, but because the branchlets have a distinct stalk I have placed it as f. *intermedia*, which, according to Börgesen, is intermediate between true *uvifera* and true *clavifera*.

(4) *Caulerpa sedoides* (R.Br.) Ag.

Harv., *Phyc. Aust.* **2**, tab. 72, 1858–63; Harv. in Hooker, *Fl. Nov. Zel.* **2**, 261, 1855; *Handb. N.Z. Flora*, p. 713, 1867; Laing, *Trans. N.Z. Inst.* 57, 132, 1926.

Erect fronds arising from a glabrous, branching, stoloniferous portion, extending to form a patch several cm. in diameter, fronds glabrous, simple, or sparsely branched, up to 20 cm. long, slightly constricted at intervals, beset with sessile branchlets, spherical or slightly obovate, lower ones distichous, subdistant, upper more densely arranged.

Caulerpa sedoides f. **novaezelandiae** form.nov.

Axe erecto ad 1·5 mm. lato, saepius ramoso quam huic speciei usitatum est, per intervalla non multum constrictis.

Erect axis thick, up to 1·5 mm. wide, cylindrical, branched more often than the type, slightly constricted at intervals, beset with densely imbricate, sessile, spherical branchlets. (Pl. 49.) Type specimen V.W.L. 54 in herb. Auckland Inst.

DISTRIBUTION. Local: Three Kings Is., Russell, Rangitoto, Narrow Neck, Kawau Is., Little Barrier Is., Noises, Fletcher's Bay, Mayor Is., Opunake, Pihama, Wellington, Happy Valley, Lyall Bay, Cook St. Endemic. General: Type species in Indian Ocean and Pacific Ocean.

Caulerpa sedoides of New Zealand differs substantially from that found in Australia and Tasmania. It would seem to differ from true f. *crassicaulis* in the greater length of the erect fronds and in the occasional slight constrictions of the axis. Svedelius (1906) maintains that f. *crassicaulis* has a truly tropical distribution and does not occur outside of tropical Australia. The longer erect fronds, the greater degree of branching and the constrictions would appear sufficient to render our plant a separate race. Further work may show that these are two races, one with densely imbricate, erect fronds and the other less dense.

(5) *Caulerpa articulata* Harv.

Harv. in Hooker, *Fl. Nov. Zel.* **2**, p. 261, 1855; *Handb. N.Z. Flora*, p. 713, 1867; Harvey-Gibson, *J. Bot., Lond.*, **31**, pl. 335, fig. 1, 1893; Laing, *Trans. N.Z. Inst.* **57**, 131, 1926.

Erect axes delicate, 6–15 mm. long, simple or scarcely branched, branching confined to the base, 1 mm. wide, constricted to give appearance of articulations; branchlets opposite, arising at the constrictions, up to 1 cm. long, distichous, cylindrical, constricted at the base; plant grass green; not adhering well to paper. (Pl. 50.) V.W.L. 176.

DISTRIBUTION. Local: Russell, Manganoui, Cape Turnagain, Lyall Bay, Island Bay and common on Wellington beaches in drift. General: Tasmania.

This is a very delicate and characteristic species.

VAUCHERIACEAE

This family is usually placed in the Siphonales. It differs from other members of the Siphonales in its reproduction and metabolism and the present author believes that its proper place is in the Xanthophyceae (Heterosiphonales).

Fronds bright green, coenocytic, aseptate, composed of long, irregularly or dichotomously branched filaments, often gregarious, forming felt-like masses attached by colourless rhizoids; chloroplasts numerous, small, without pyrenoids, monoecious or dioecious; oogonia sessile or pedicellate, globular to ovoid, bearing a single, uninucleate ovum; antheridia varied in shape, sessile, stalked or borne on a special colourless cell, emitting small biciliate antherozoids; reproduction by compound zoospores, formed at the end of branches; thick-walled akinetes formed within the filaments; aplanospores large, ellipsoidal, formed at the end of the branches.

Vaucheria DC.

Filaments continuous, without constrictions; reproduction as indicated for the family.

1. Antheridia borne on a special stalk cell (androphore). *V. synandra*
   Antheridia not borne on a special stalk cell. **2**
2. Antheridia egg-shaped or pyriform. *V. thuretii*
   Antheridia hooked or circinate. **3**
3. Filaments 65–85μ dia. *V. sessilis*
   Filaments 96–105μ dia. *V. pseudosessilis*

(1) *Vaucheria thuretii* Woron.

Harv., *Phyc. Brit.* tab. 321, 1849–51; Newton, *Handb. Brit. Seaw.* p. 102, 1931.

Filaments 60–122μ broad, rarely as small as 30μ; oogonia and antheridia on the same filament; oogonia borne singly, ovoid or pyriform, shortly stalked, rarely sessile, 130–300μ wide; oospore 120–240μ; antheridia erect or horizontal, ovoid or pyriform, 40–80 × 60–150μ; aplanospores borne terminally on short lateral branches. (Fig. 152.)

DISTRIBUTION. Local: Salt marshes and mangrove swamps. General: Europe, Mediterranean, Atlantic North America.

(2) *Vaucheria synandra* Woron.

Newton, *Handb. Brit. Seaw.* p. 103, 1931.

Filaments 50–100μ (usually 88μ) dia., antheridia horn-shaped, 2–7 borne on a swollen androphore which itself is borne on a small colourless cell cut off from the main coenocyte; oogonia lateral, almost spherical, borne on the same filament as the antheridia, 100–110μ dia.; oospore spherical. (Fig. 152.)

Distribution. Local: Narrow Neck. General: Europe.

The one plant is referred here with some doubt because only oogonia were found. The measurements of the oogonia and of the filaments agreed with the description above.

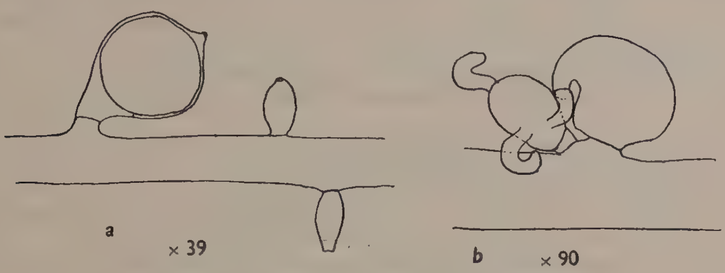

Fig. 152. *a, Vaucheria thuretii. b, V. synandra.*

(3) *Vaucheria sessilis* (Vauch.) DC.

Kütz., *Tab. Phyc.*, **6**, tab. 59, fig. 2, 1856; West, *Alg.* **1**, p. 246, fig. 159, 1916.

Filaments 65–85μ wide; oogonia and antheridia borne on the same filaments; oogonia borne singly or in pairs, ovoid or oblong ovoid, 70–85 × 75–100μ, more or less oblique with a short beak; antheridium between the oogonia or beside the oogonium, pedicellate, straight or hooked; ripe oospore spotted, golden brown; zoosporangia ovoid-clavate, terminal on a short branch; zoospore 110–145μ dia. (Fig. 153.)

Distribution. Local: Shoal Bay on salt marsh (Auckland), and probably elsewhere. General: Europe, U.S.A.

In general appearance this species is very like the next.

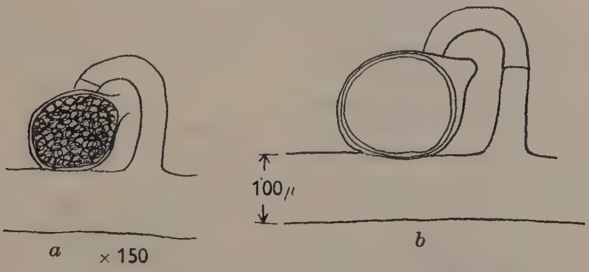

Fig. 153. *a, Vaucheria sessilis. b, V. pseudosessilis.*

(4) **Vaucheria pseudosessilis** sp.nov.

Thallus filamentorum ramosorum, 96–105μ latus, oogoniis simplicibus, sessilibus, ovoidibus aut oblongo-ovoidibus, 70–75μ × 118–122μ, plus minusve obliquis, cum rostro brevi; antheridio ab oogonio simplici, ex brevi cauli, adunco aut circinato; oosporo maturo aureo fulvo, oogonium complens.

Thallus consisting of branched filaments 96–105μ wide; oogonia single, sessile, ovoid or oblong ovoid, 70–75 × 118–122μ, more or less oblique, with short beak; antheridium beside the single oogonium, on a short pedicel, hooked or circinate; ripe oospore golden brown, filling the oogonium. (Fig. 153.) Type specimen in Herb. Lindauer.

Distribution. Local: Bayswater and probably elsewhere.

This species is very like *V. sessilis* from which it differs in the greater width of the filaments, 96–105μ as against 50–85μ, the single oogonia instead of the common paired oogonia of *V. sessilis*, and the golden brown unspotted ripe oospores.

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  sessilis, 495
  synandra, 494
  thuretii, 494
Vaucheriaceae, 374, 494

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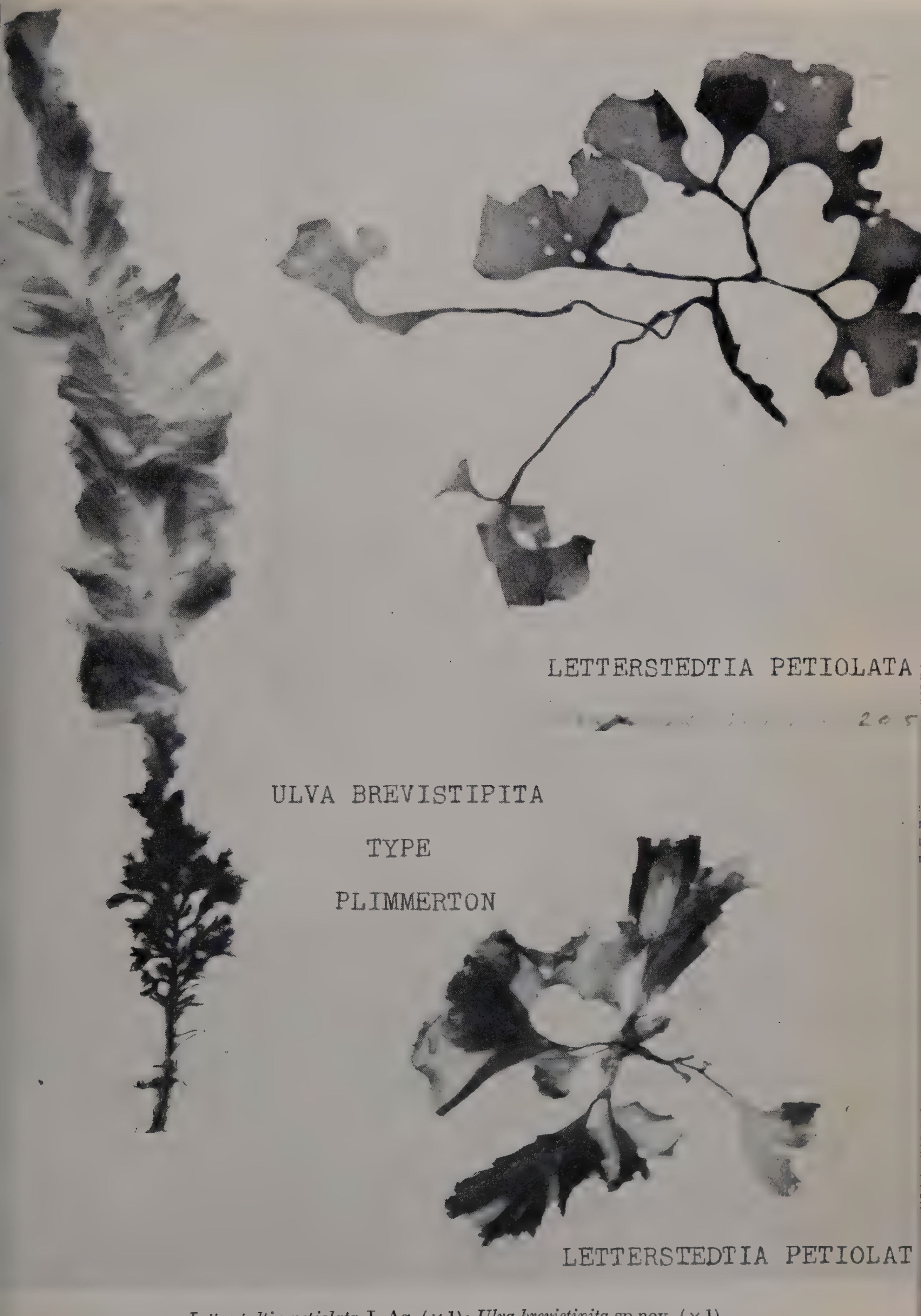
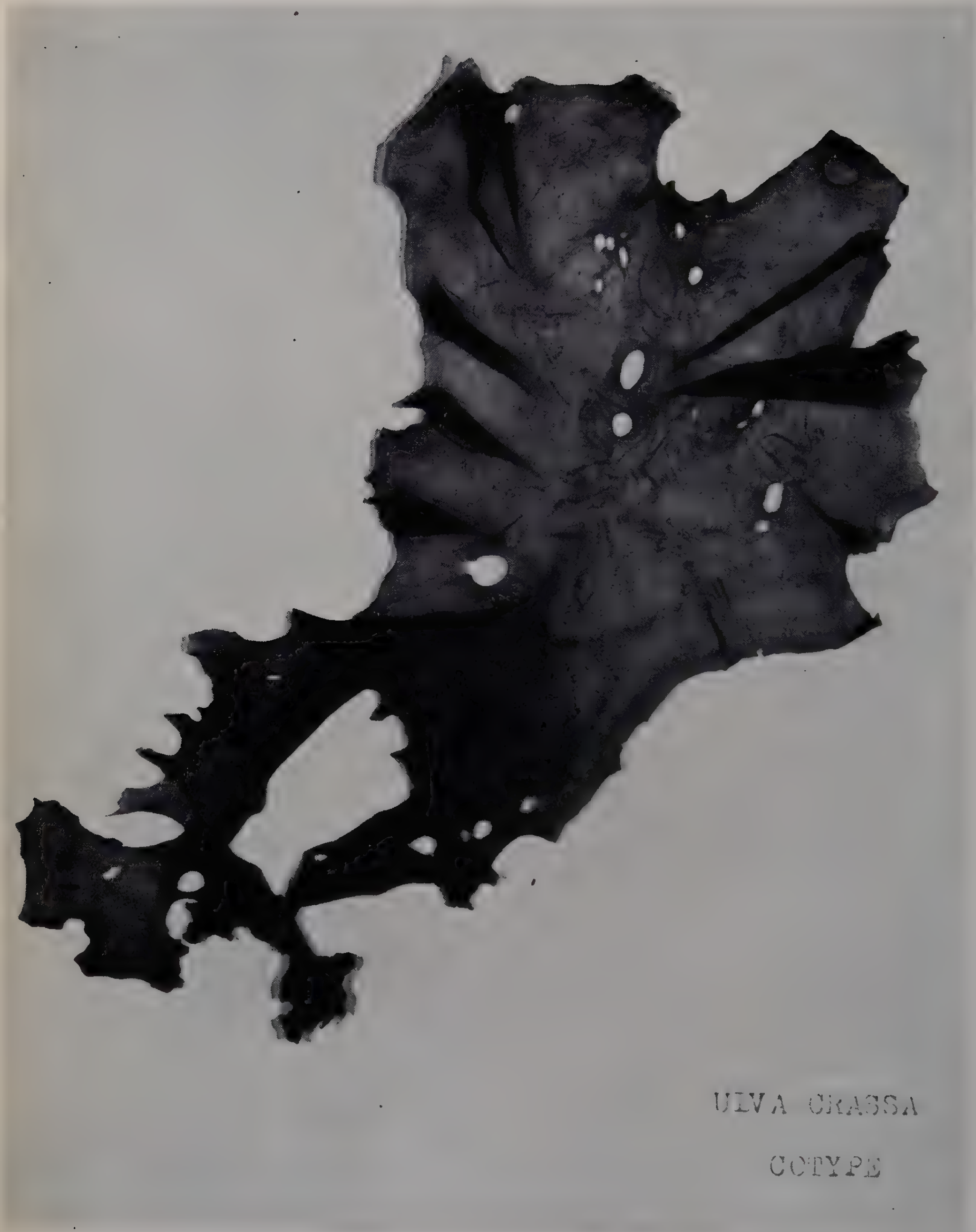
  salina, 469
Wittrockiellaceae, 439, 469

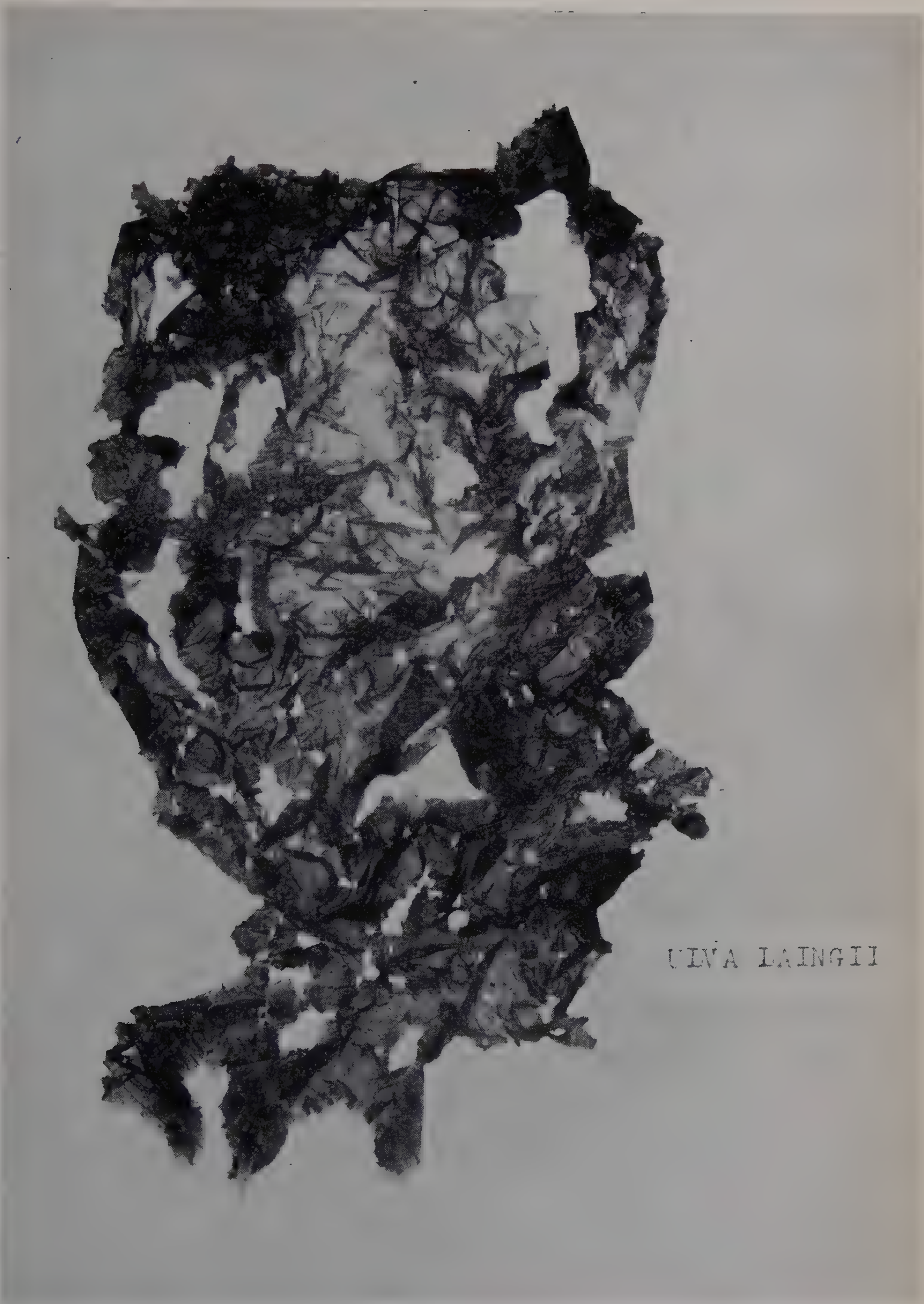
Xenococcus schousboei, 352



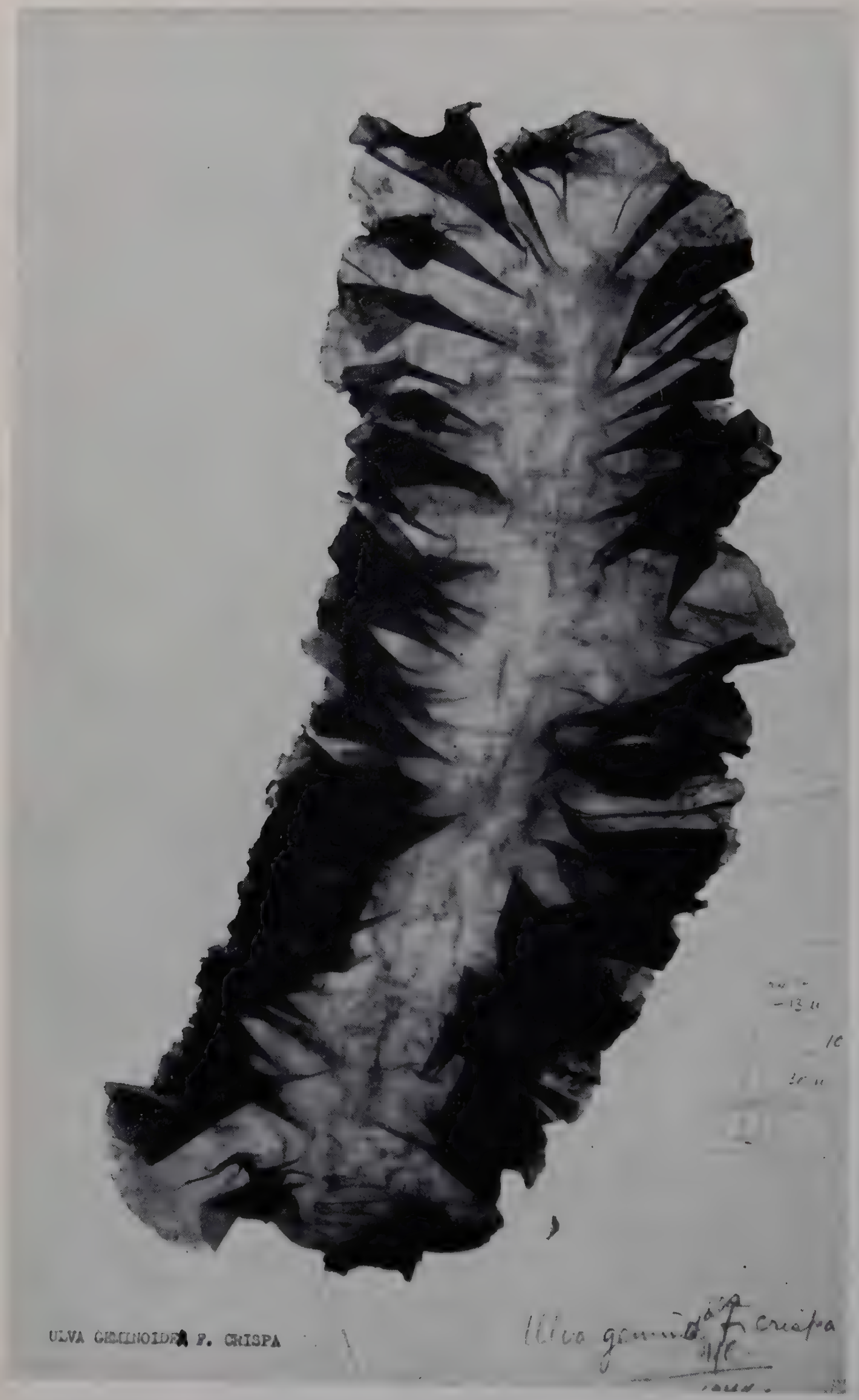
Letterstedtia petiolata J. Ag. (× 1); *Ulva brevistipita* sp.nov. (× 1).



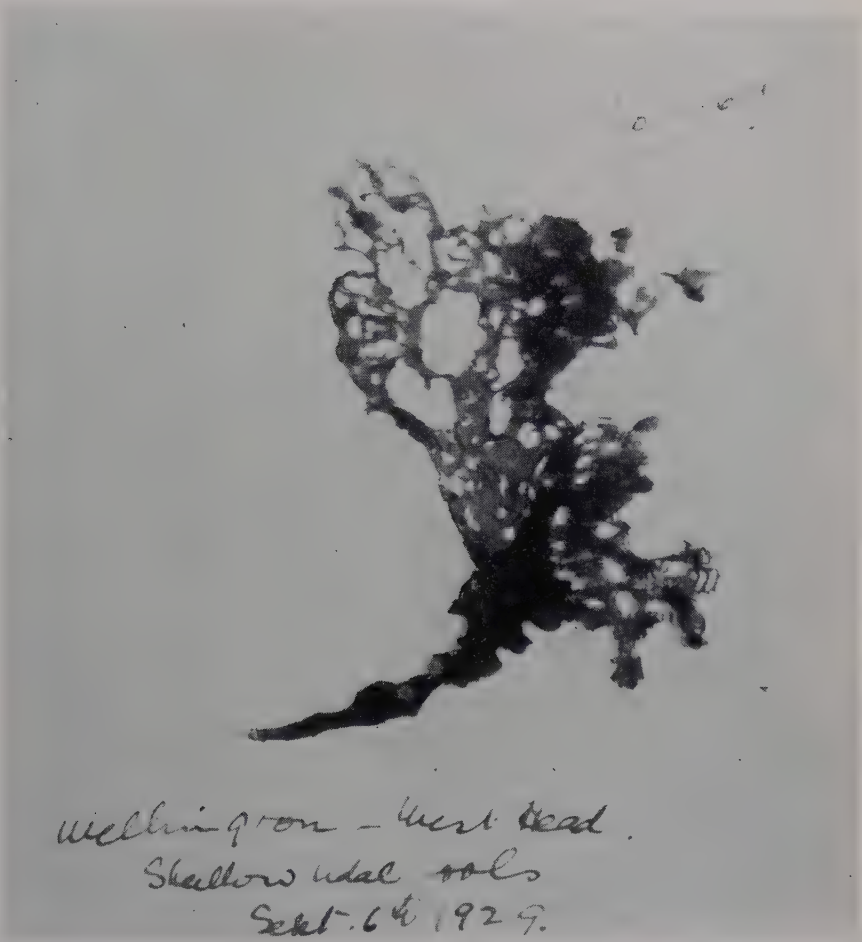
Ulva crassa sp.nov. (× 1).



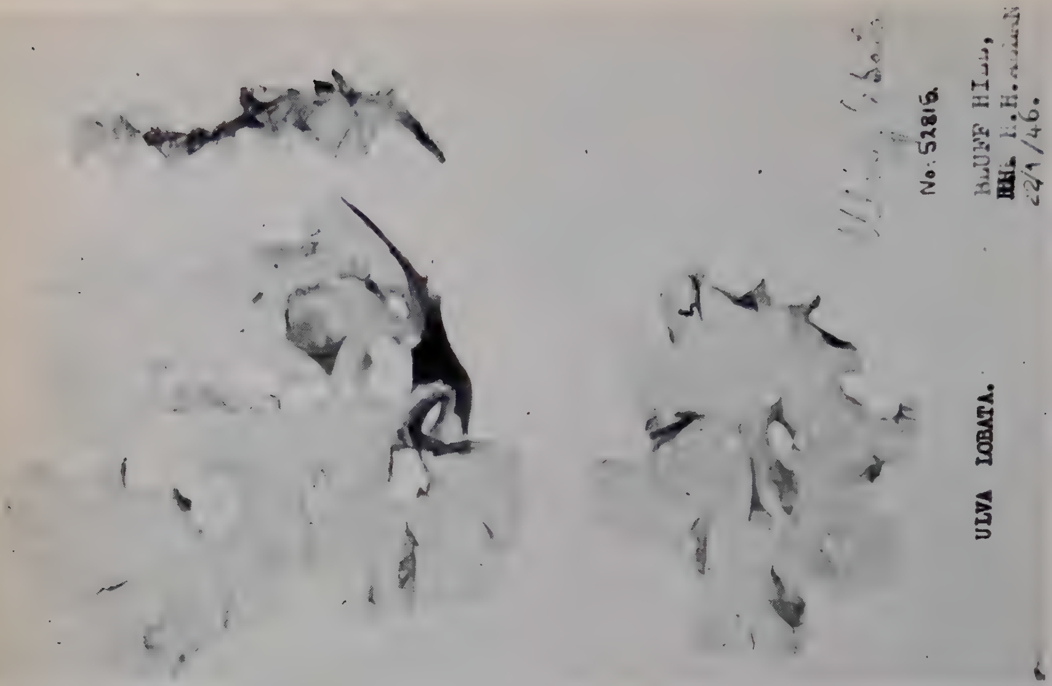
Ulva laingii sp.nov. (× $\frac{2}{3}$).

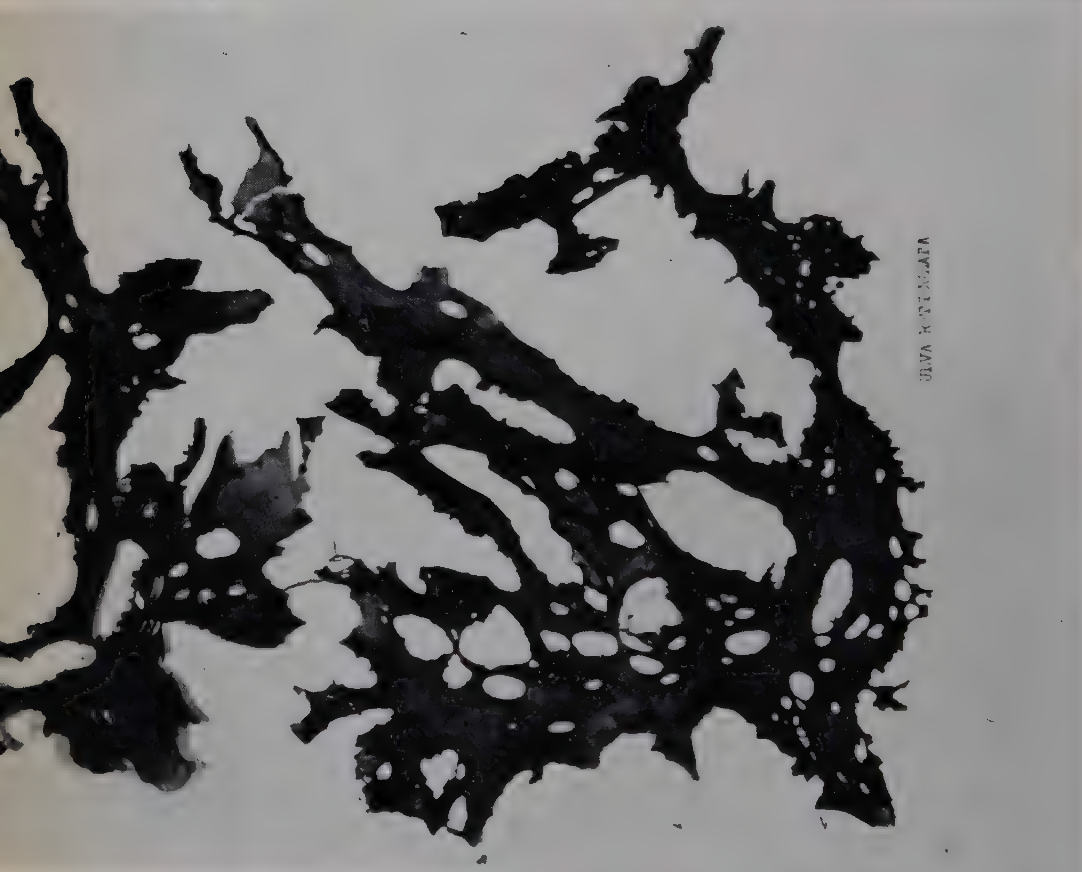


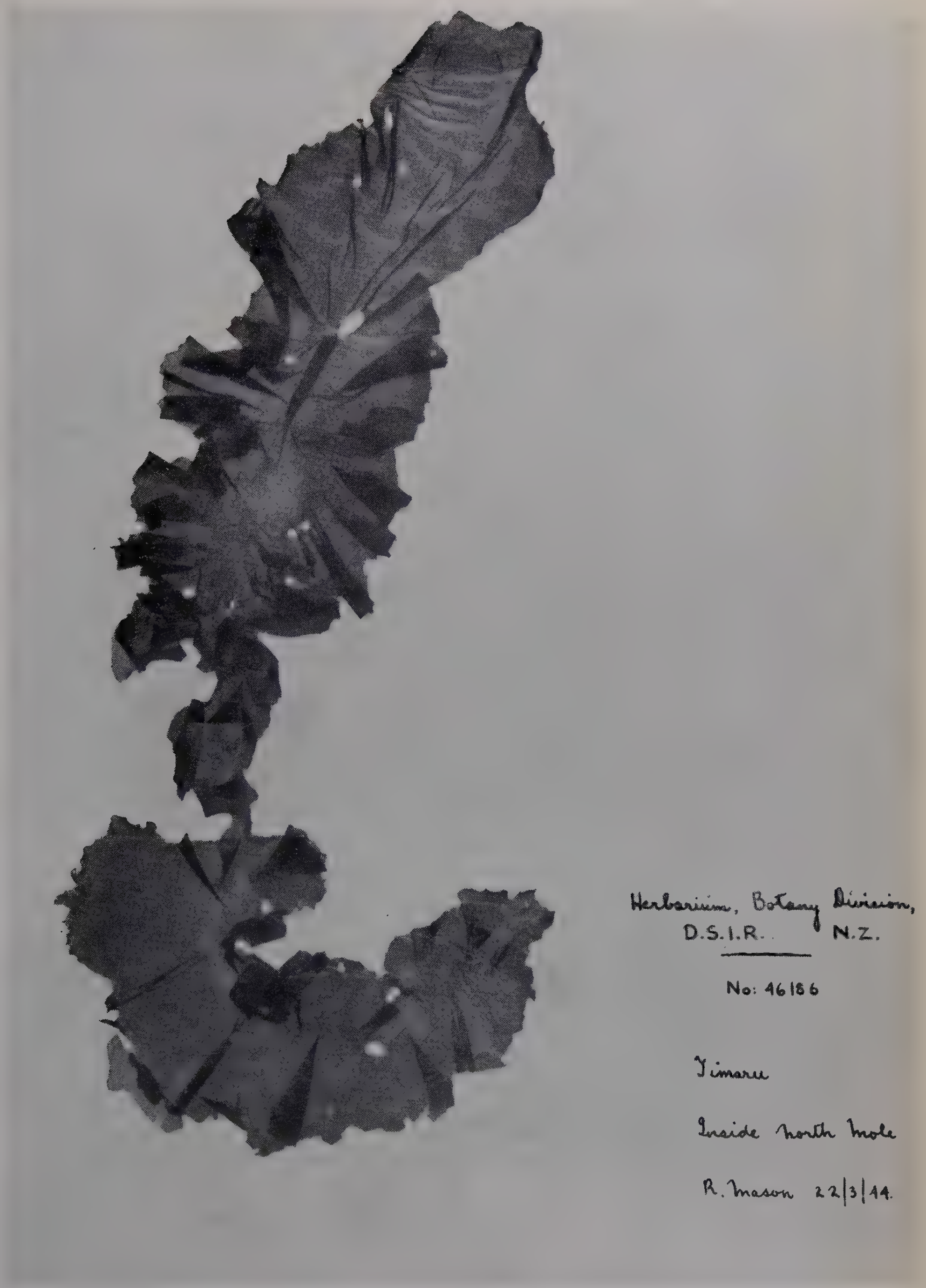
Ulva geminoidea var. *crispa* var. nov. (×⅔).



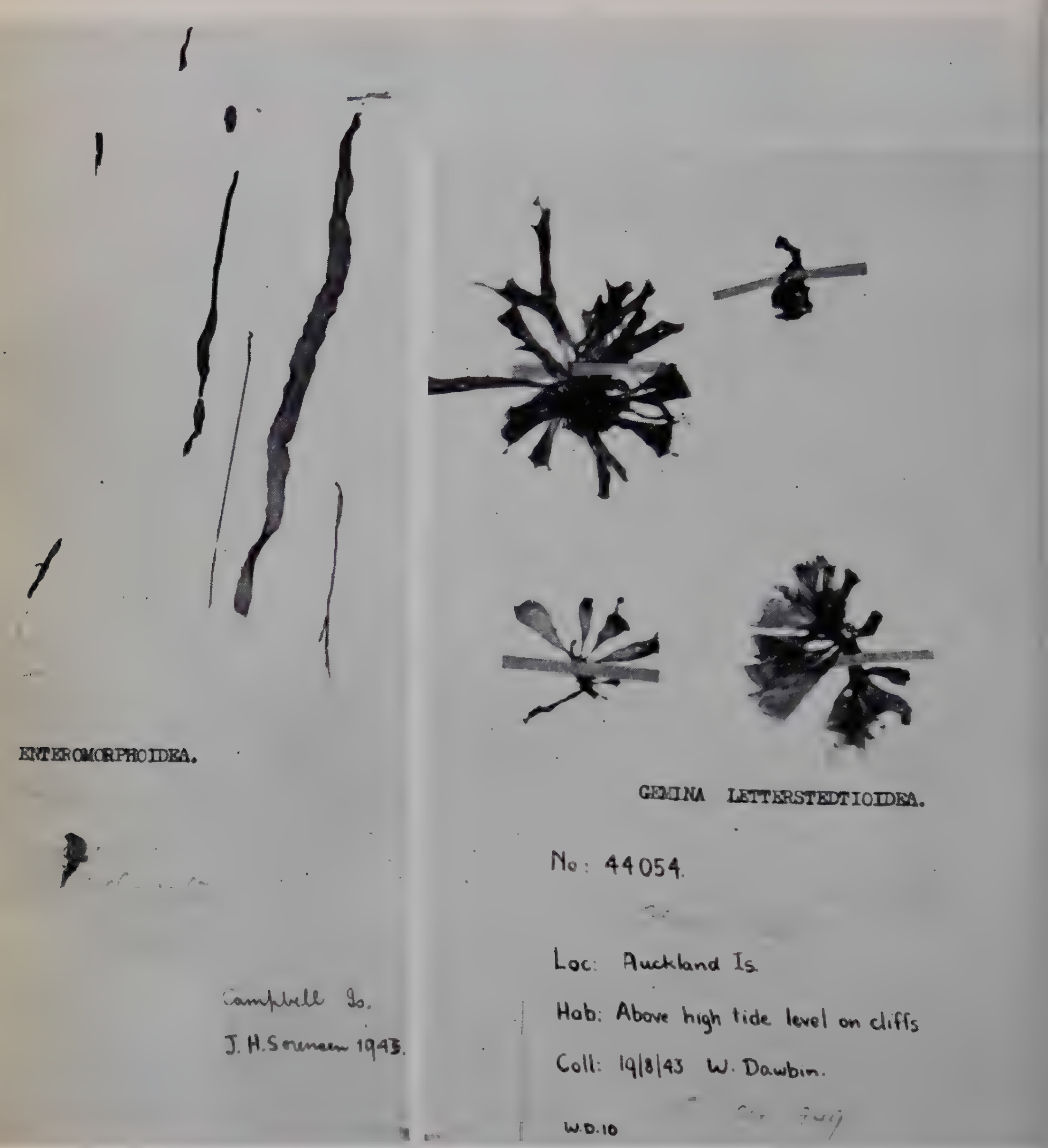
Ulva geminoidea var. *dentata* var. nov. (× 1).


No. 52815.
BLUFF HI...,
HH. E.H. ...
22/1/46.
ULVA LOBATA.

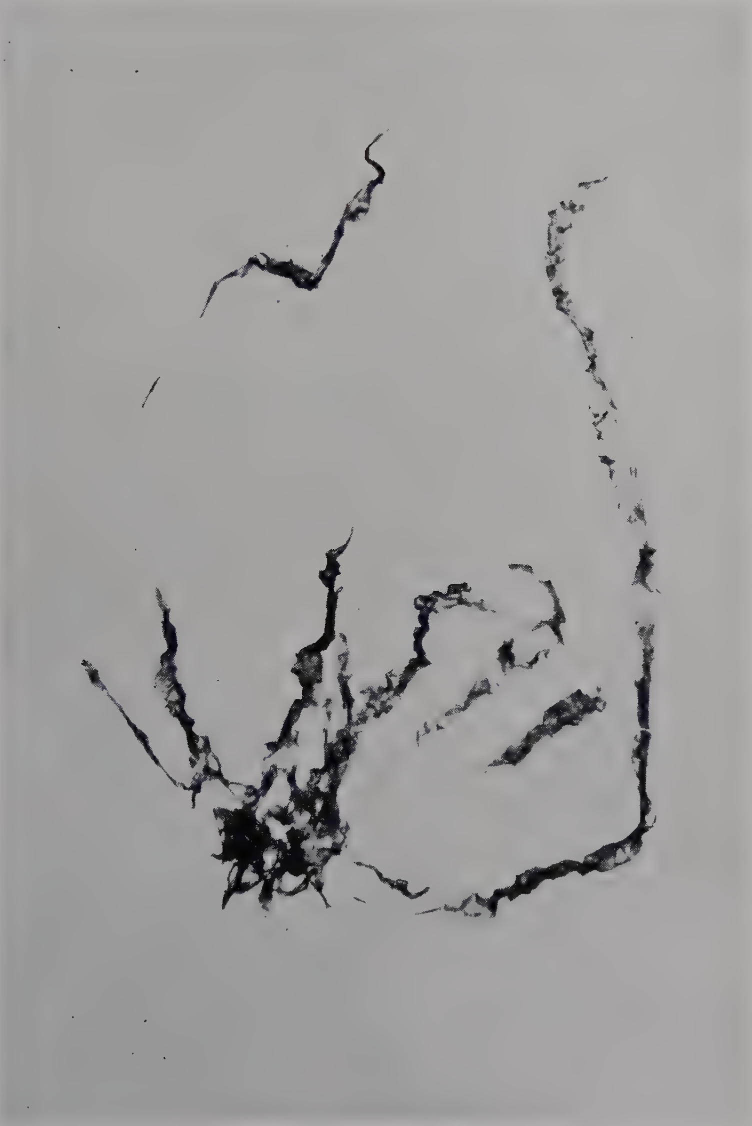

ULVA RETICULATA



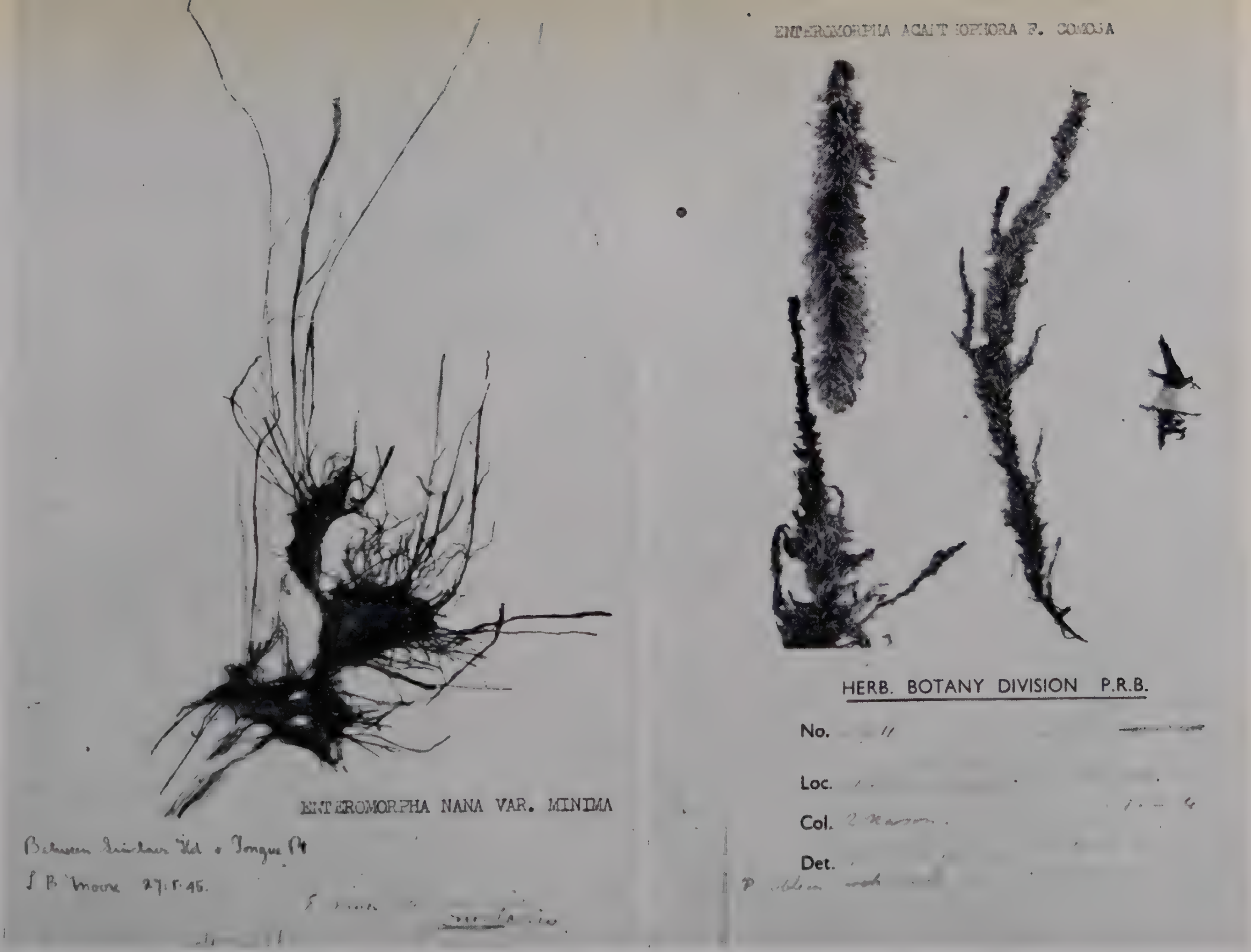
Lobata foliosa Chapm. (× $\frac{3}{4}$).



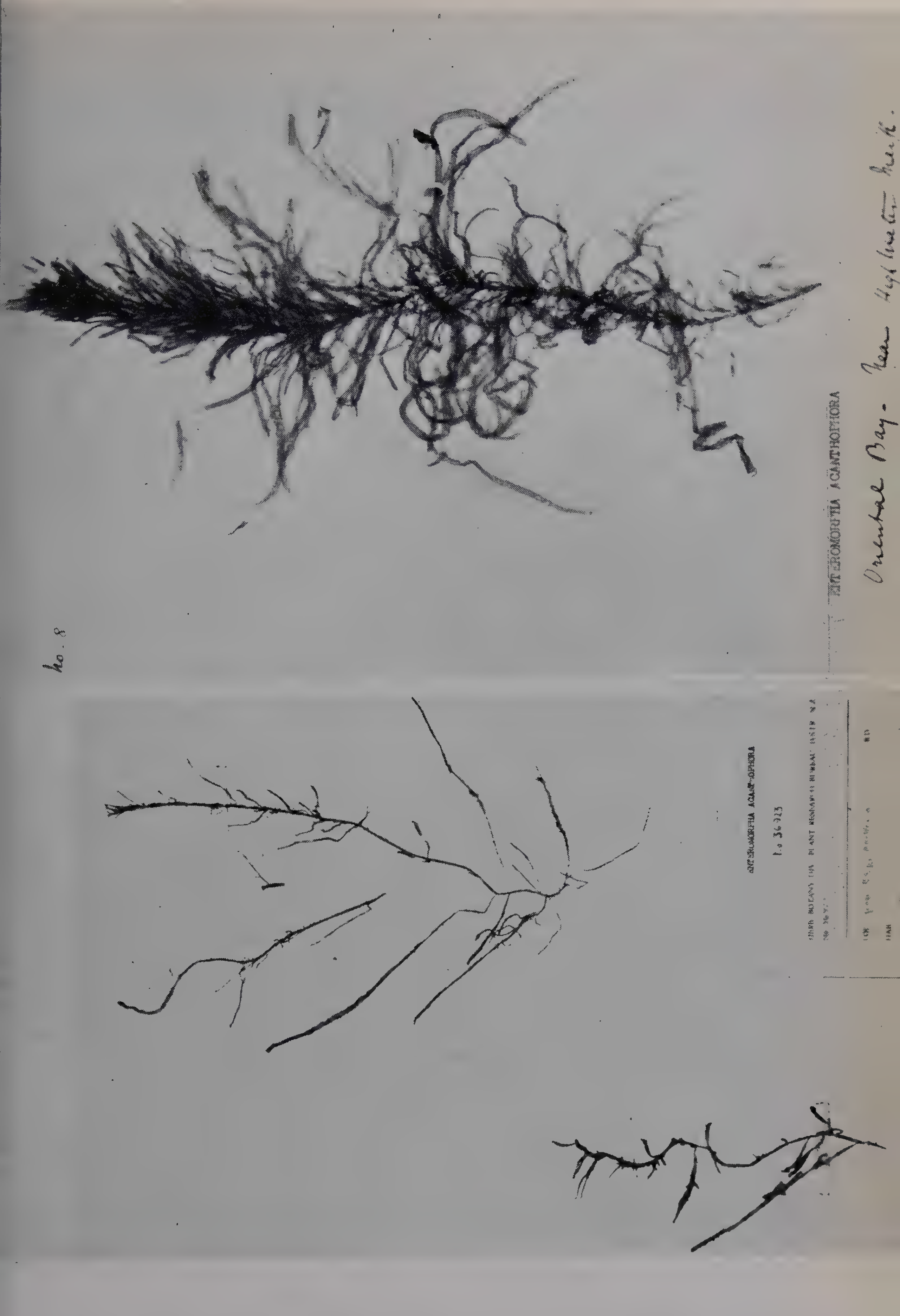
Top left: *Gemina enteromorphoidea* Chapm. ($\times \frac{2}{3}$); Bottom left: *Gemina clavata* Chapm. ($\times \frac{2}{3}$). Right: *Gemina letterstedtioidea* Chapm. ($\times \frac{2}{3}$).

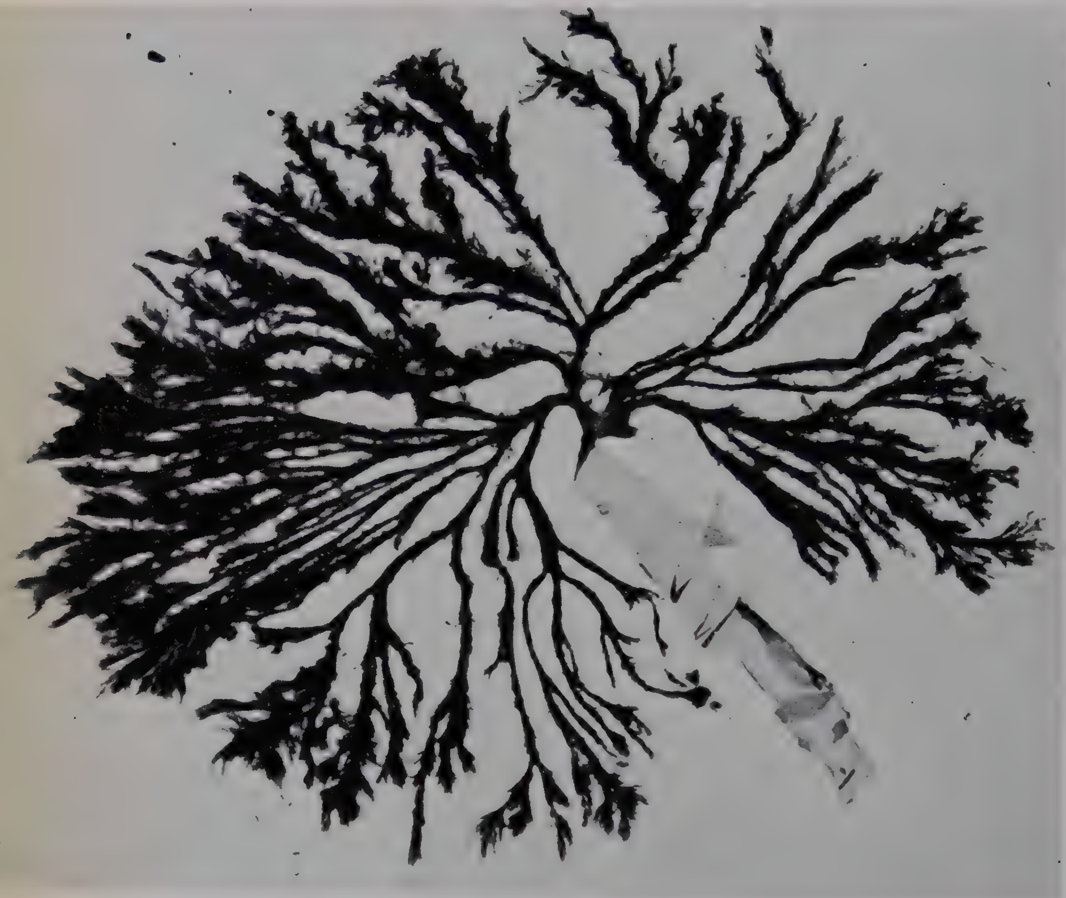


Enteromorpha compressa var. *biattenuata* var.nov. (× $\frac{2}{3}$).

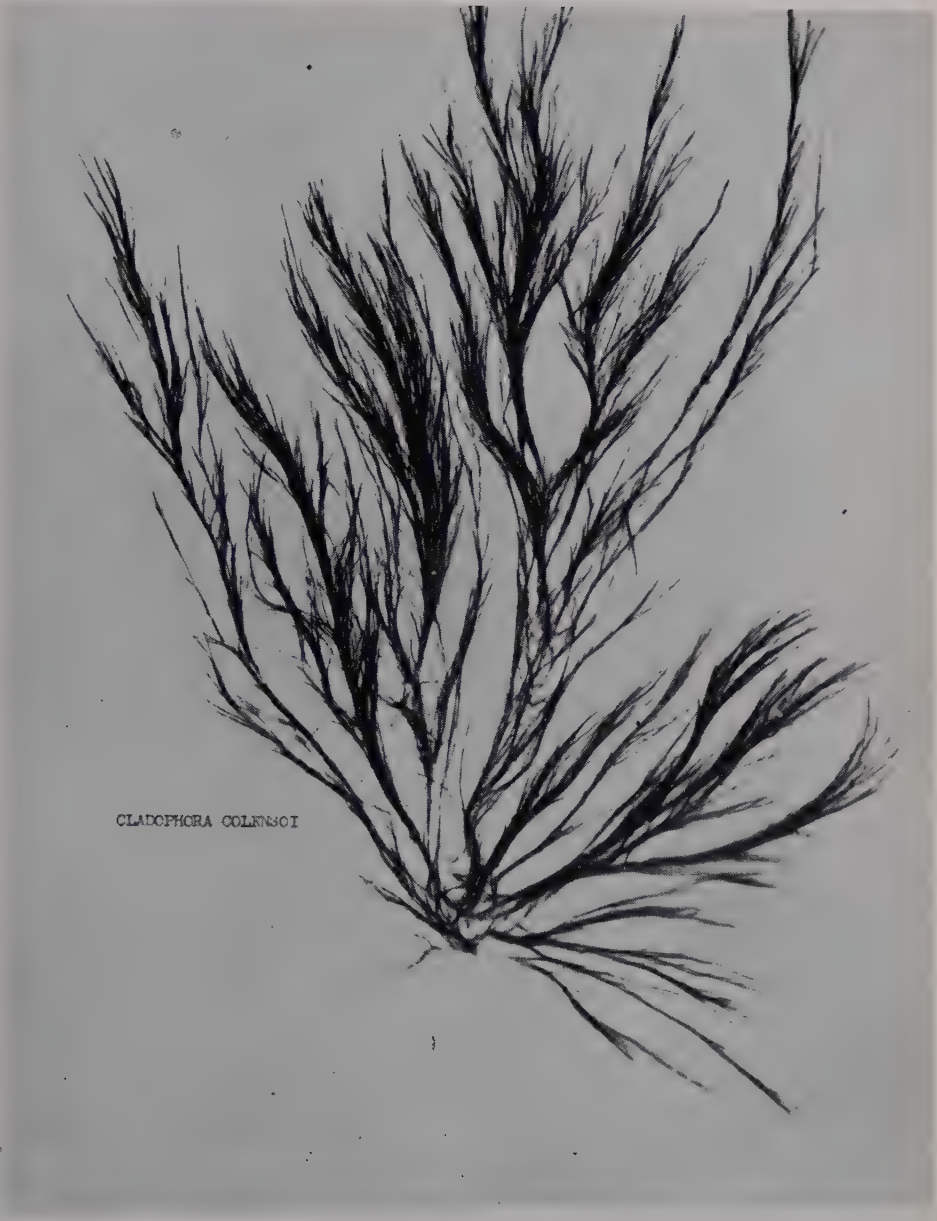

ENTEROMORPHA NANA VAR. MINIMA
Between Sinclair Hd & Tongue Pt
J B Moore 27.5.45.
ENTEROMORPHA ACANTHOPHORA F. COMOSA
HERB. BOTANY DIVISION P.R.B.
No.
Loc.
Col.
Det.

Left: *Enteromorpha nana* var. *minima* ecad *rivularis* (Collins) comb.nov. (×$\frac{2}{3}$). Photograph of an unusual plant from Sinclair Head (see text). Right: *Enteromorpha ramulosa* var. *acanthophora* ecad *comosa* ecad nov. (×$\frac{2}{3}$)

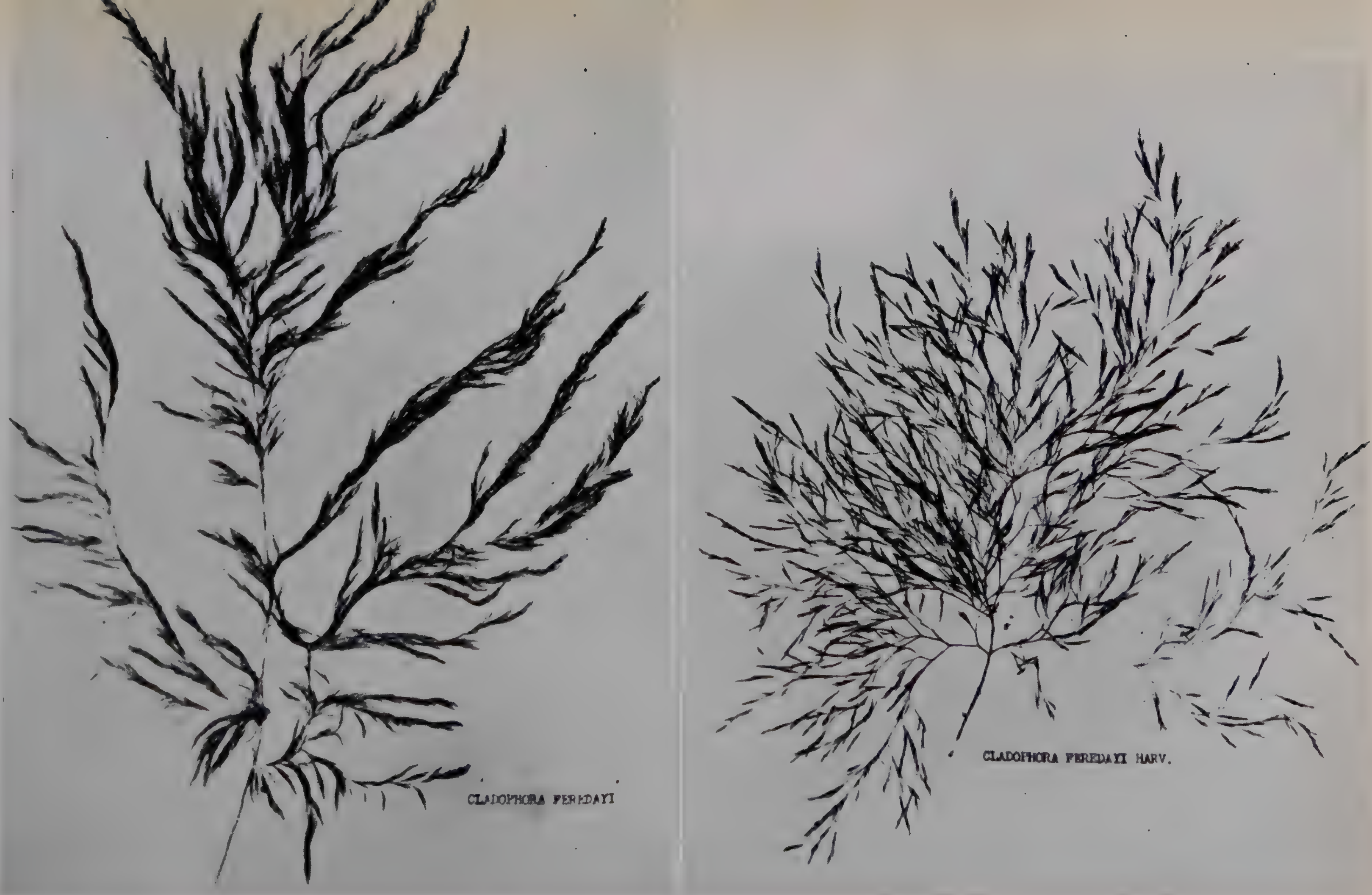

ENTEROMORPHA ACANTHOPHORA
Oriental Bay. Near high water mark.
No. 8
ENTEROMORPHA ACANTHOPHORA



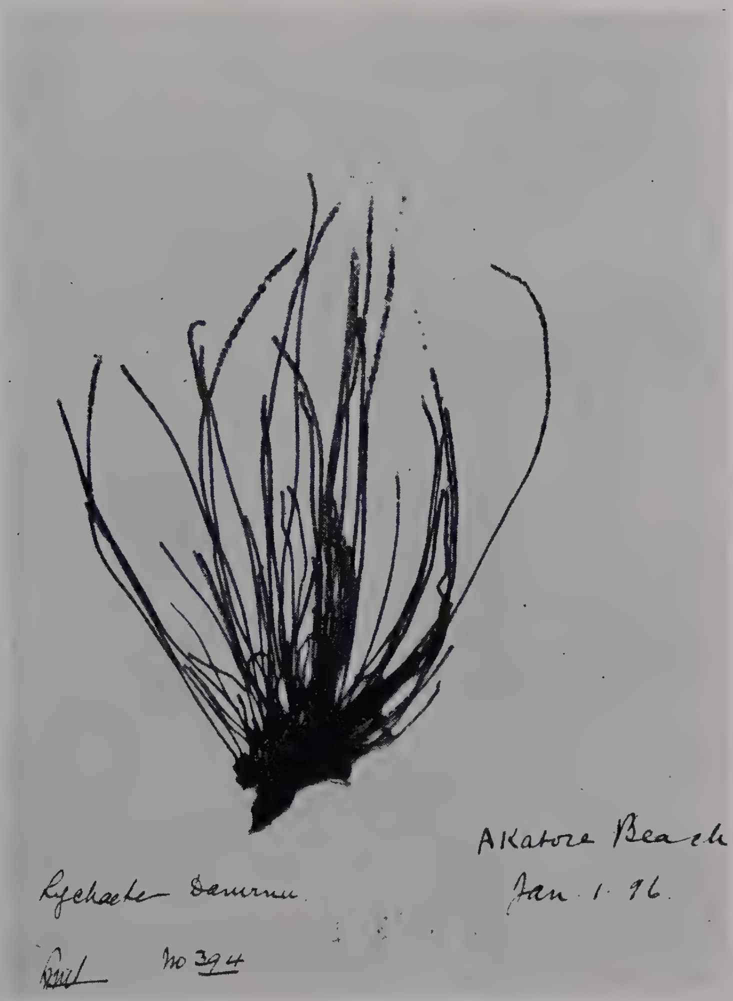
Acrosiphonia pacifica Kütz. (× $\frac{2}{3}$)



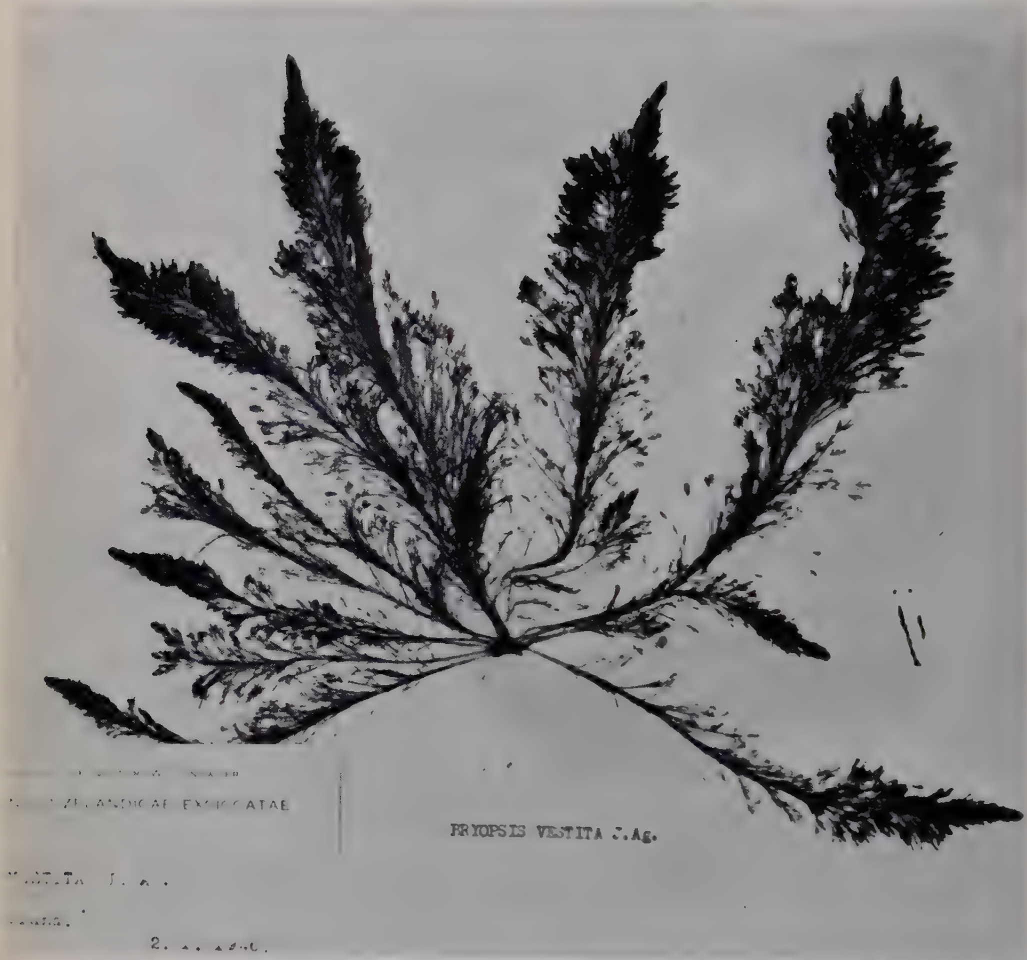
Cladophora colensoi Harv. (× $\frac{2}{3}$).



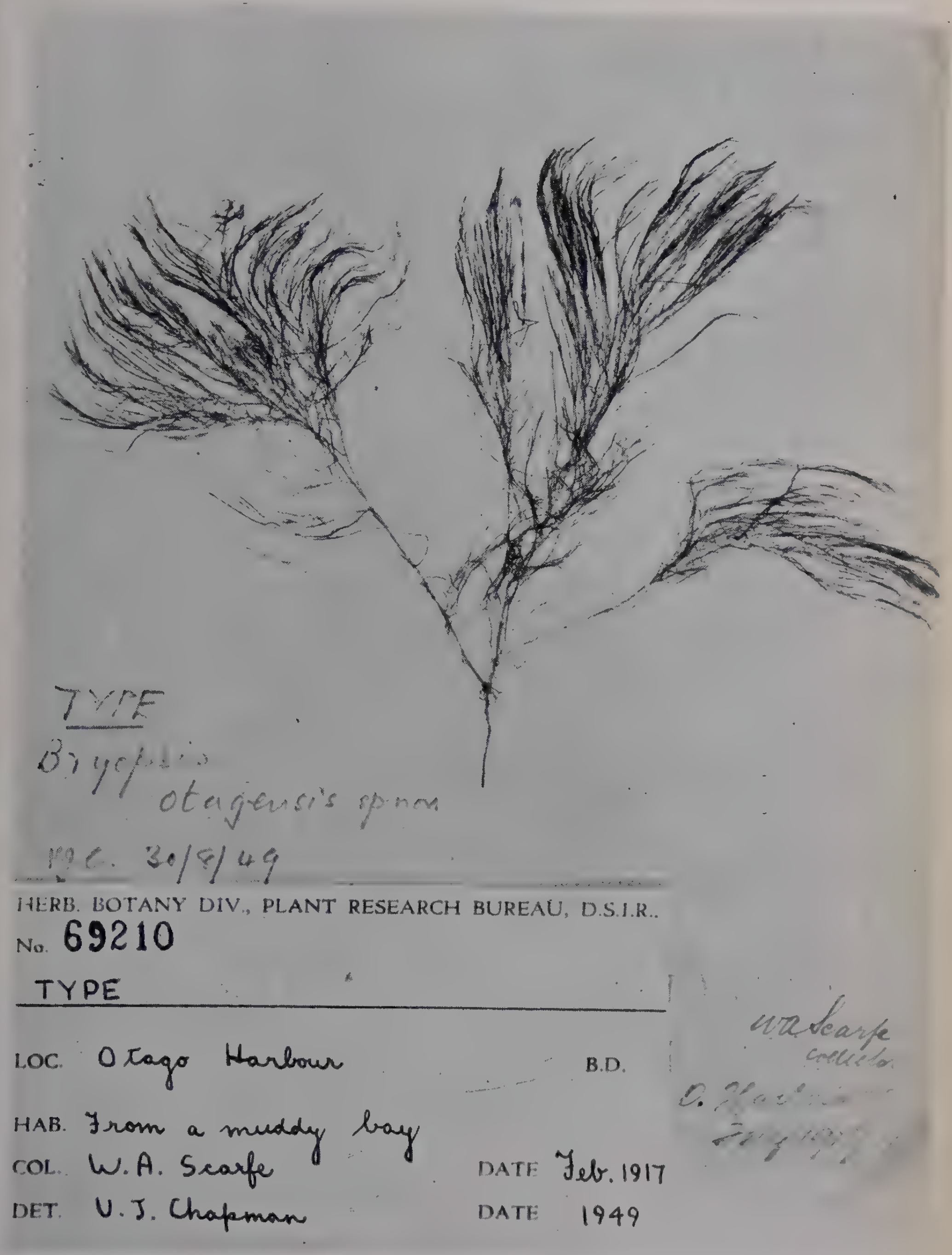
Two forms of *Cladophora feredayi* Harv.



Chaetomorpha darwinii f. *stricta* form.nov. (× $\frac{2}{3}$).



Bryopsis vestita f. *laxa* form.nov. ($\times\frac{2}{3}$)

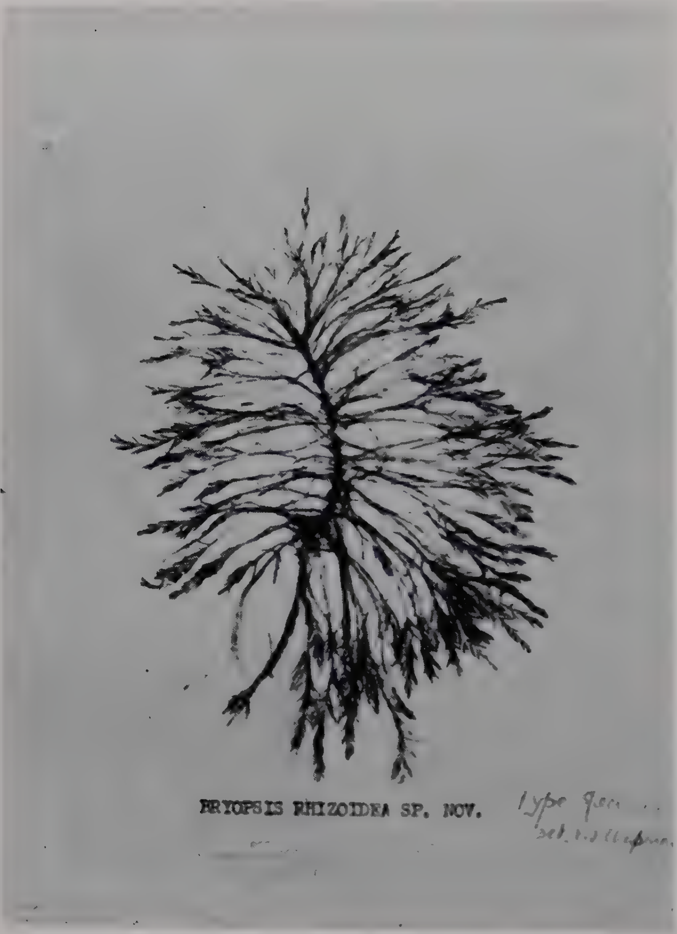


TYPE
Bryopsis
otagensis sp.nov
V.J.C. 30/8/49

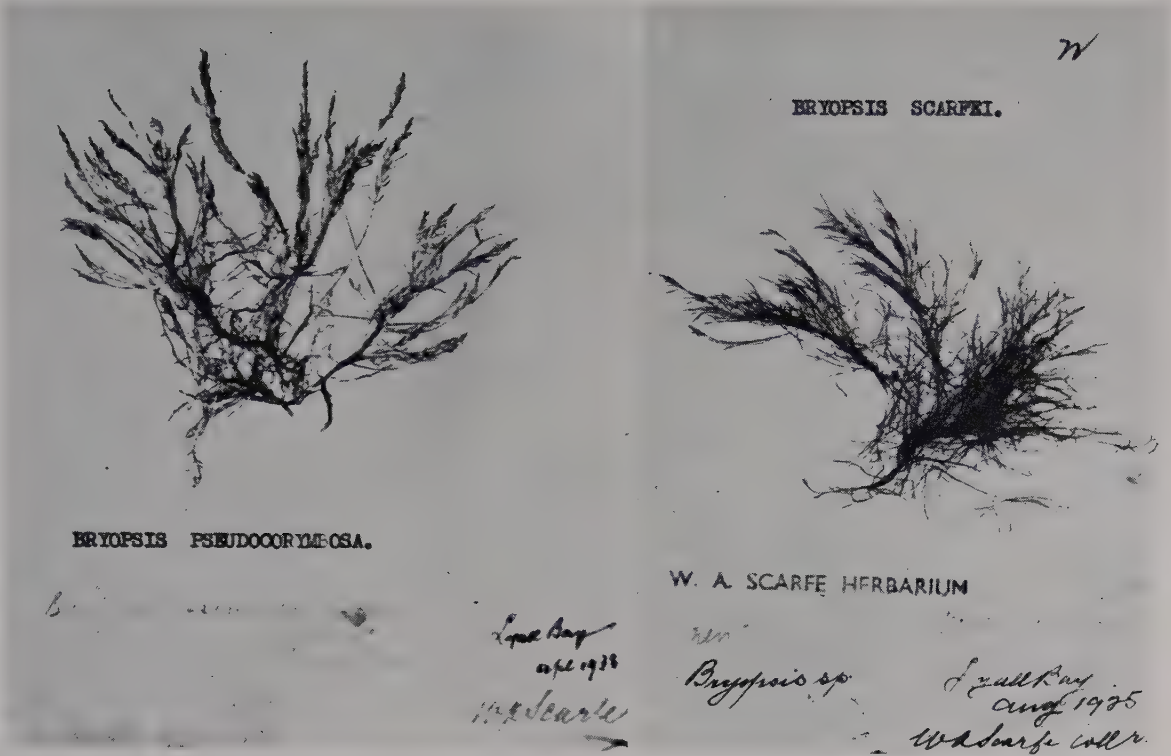
HERB. BOTANY DIV., PLANT RESEARCH BUREAU, D.S.I.R.
No. 69210
TYPE
LOC. Otago Harbour B.D.
HAB. From a muddy bay
COL. W.A. Scarfe DATE Feb. 1917
DET. V.J. Chapman DATE 1949

W.A. Scarfe
collector
O. Ha[illegible]
[illegible]

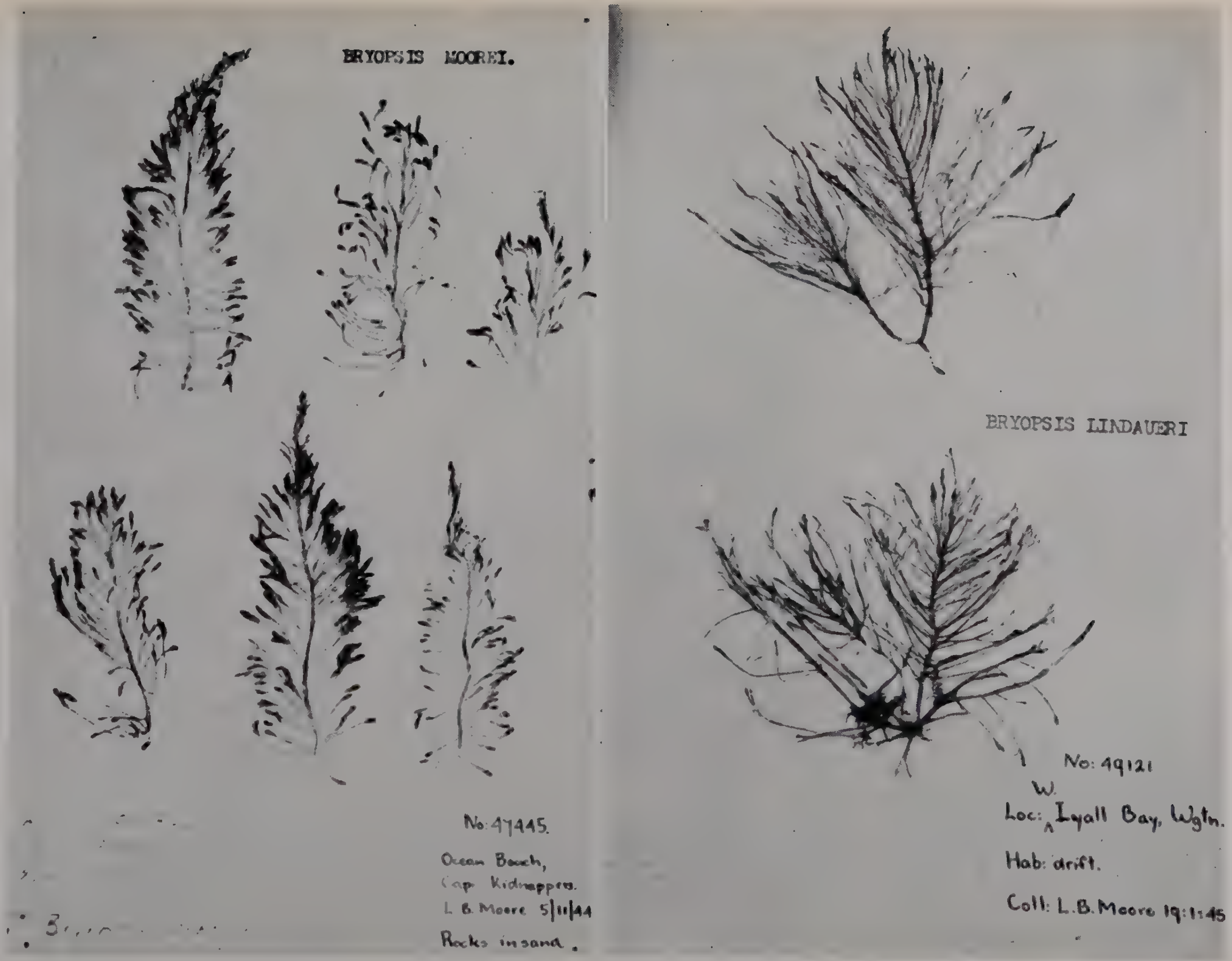
Bryopsis otagensis sp.nov. (×⅔).



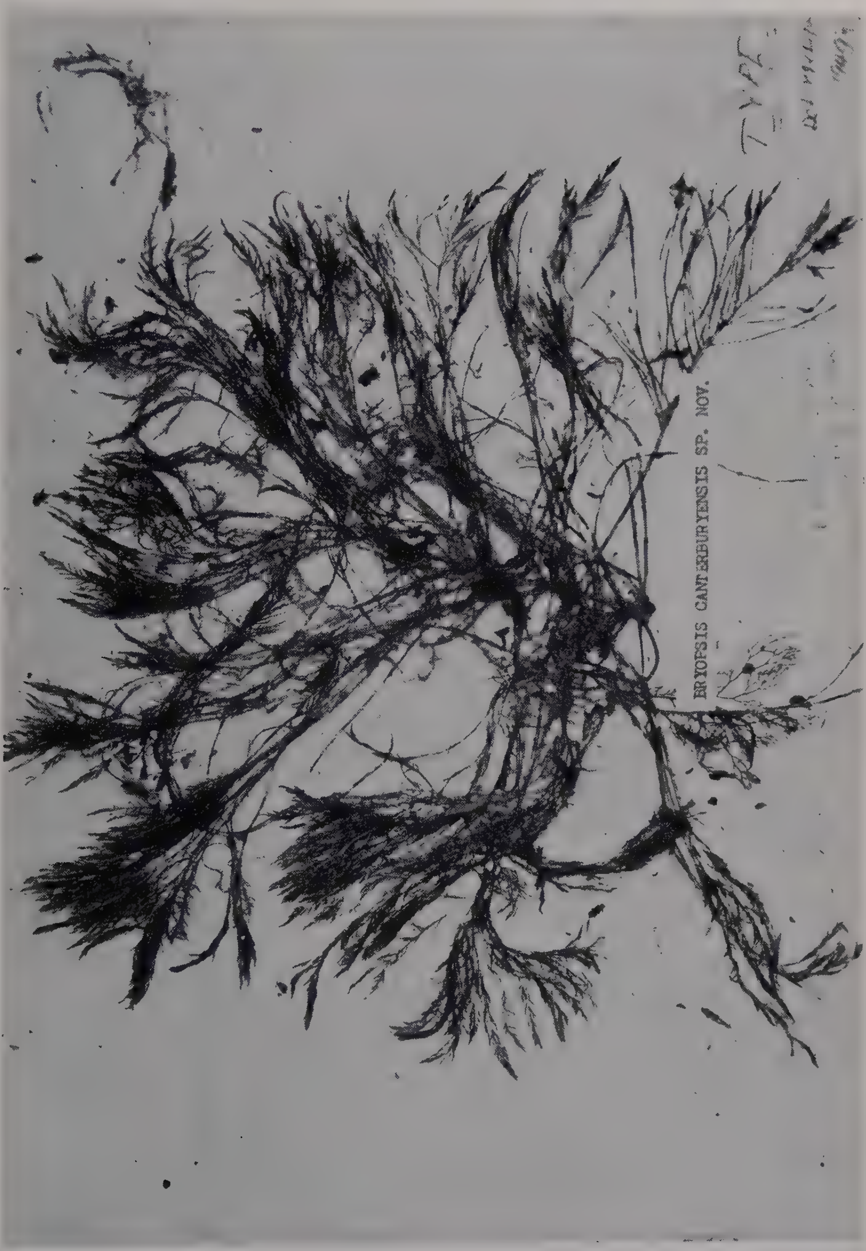
Bryopsis rhizoidea sp.nov. (× ⅔).


BRYOPSIS PSEUDOCORYMBOSA.
Lyall Bay apl 1938 W A Scarfe
W
BRYOPSIS SCARFEI.
W. A. SCARFE HERBARIUM
Bryopsis sp.
Lyall Bay aug 1935 WA Scarfe coll.

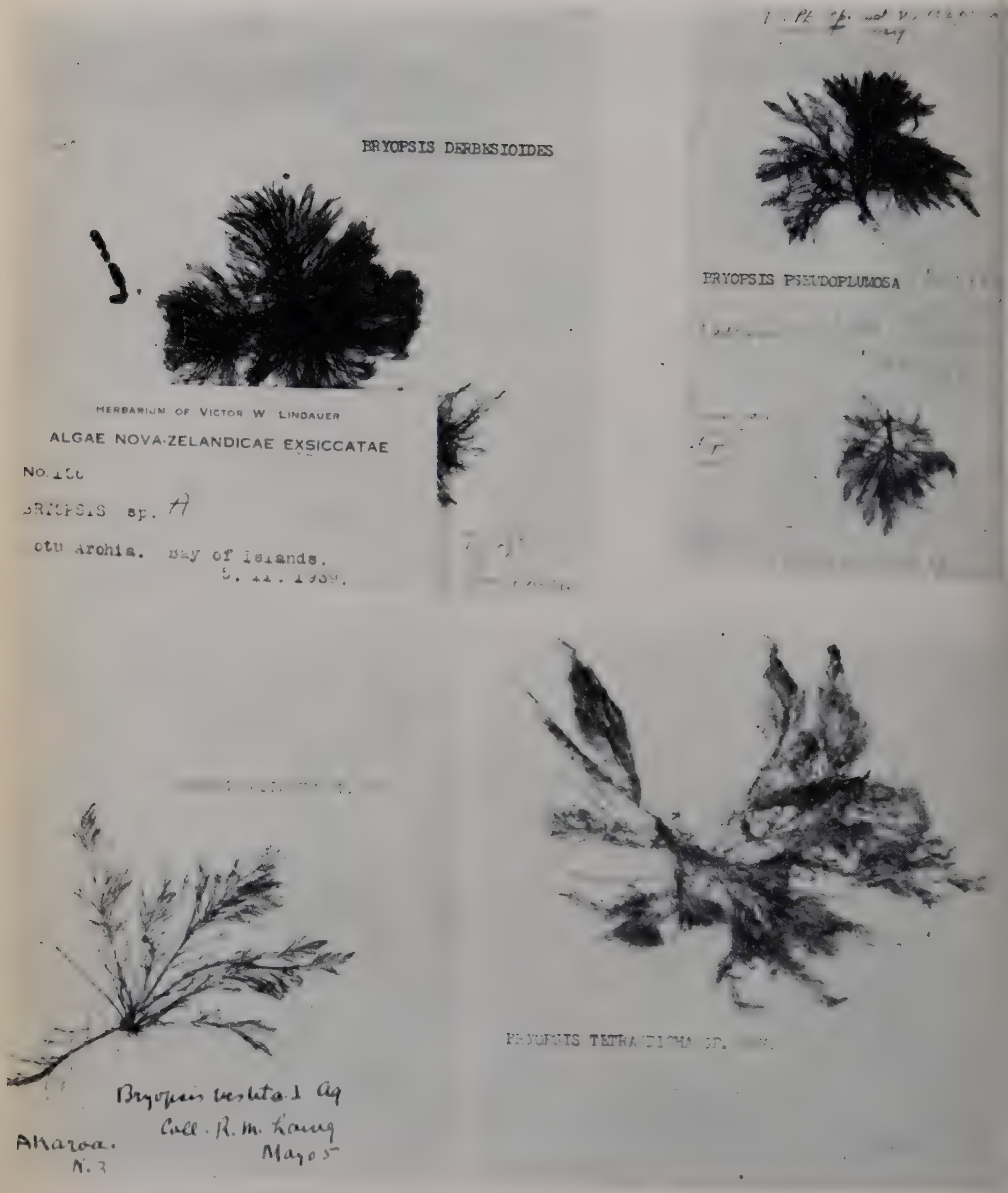
Left: *Bryopsis pseudocorymbosa* sp.nov. ($\times \frac{2}{3}$). Right: *Bryopsis scarfei* sp.nov. ($\times \frac{2}{3}$).



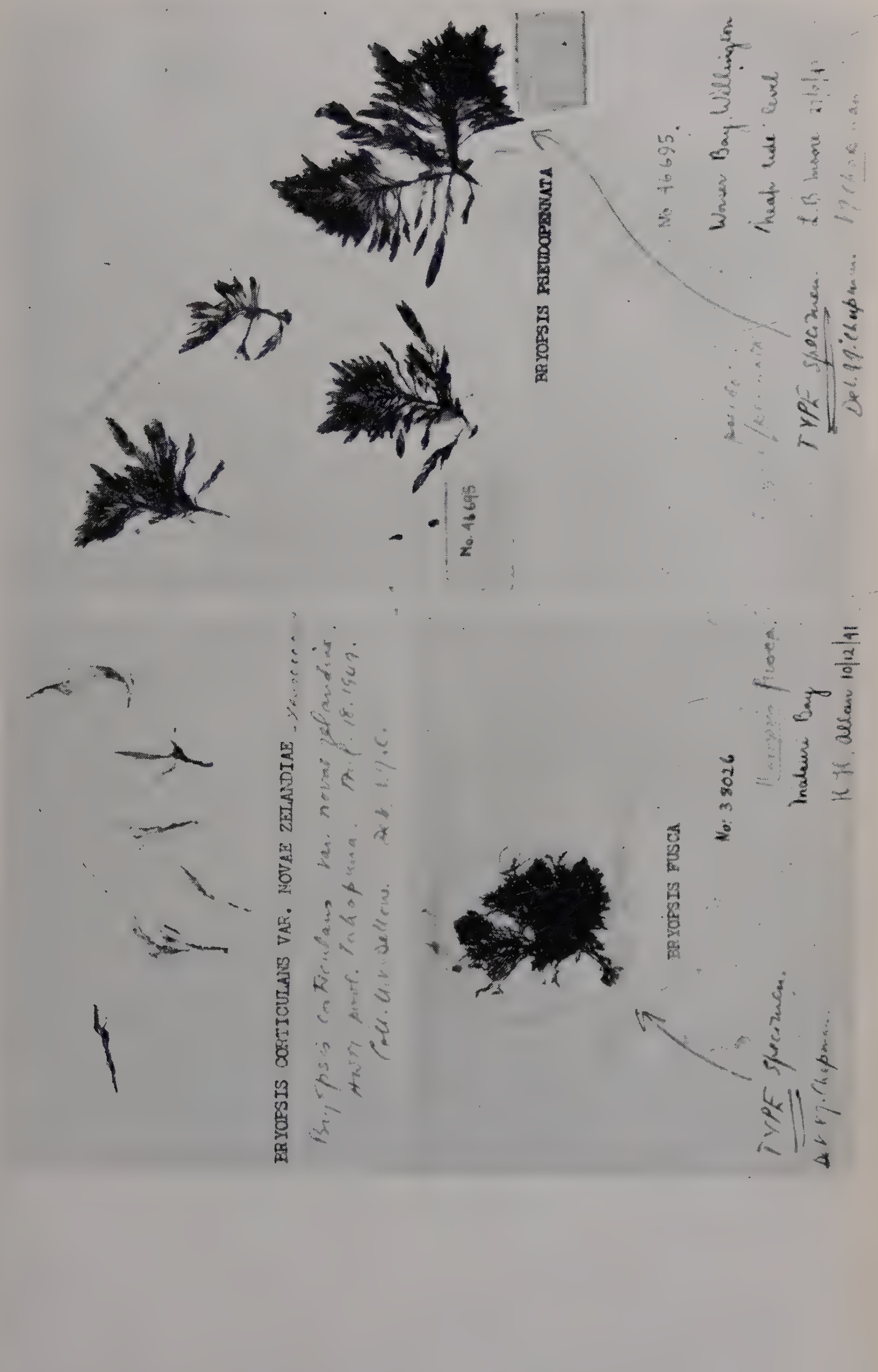
Left: *Bryopsis moorei* sp.nov. (×$\frac{2}{3}$). Right: *Bryopsis lindaueri* sp.nov. (×$\frac{2}{3}$).



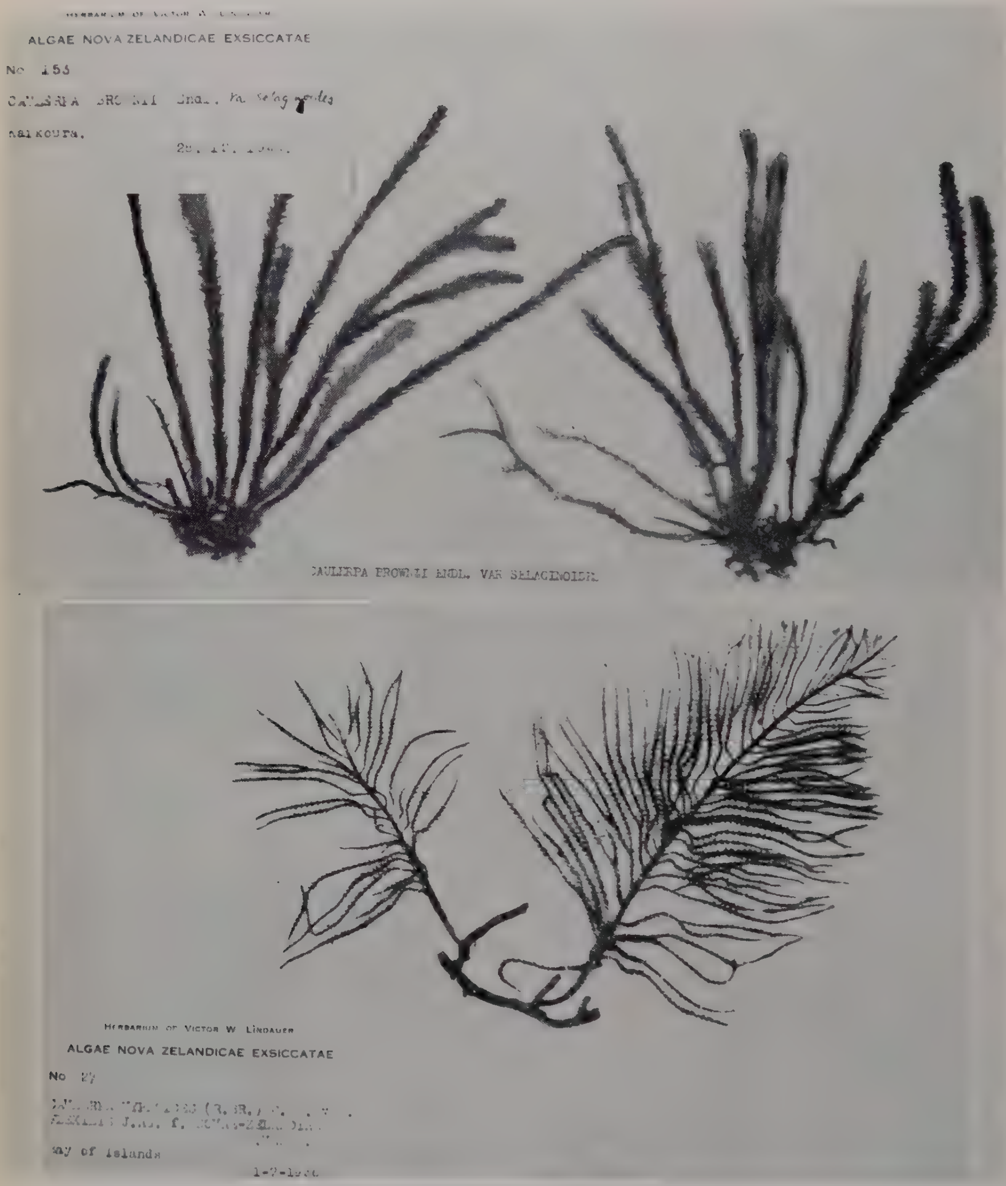
Bryopsis canterburyensis sp.nov. $(\times \frac{2}{3})$.



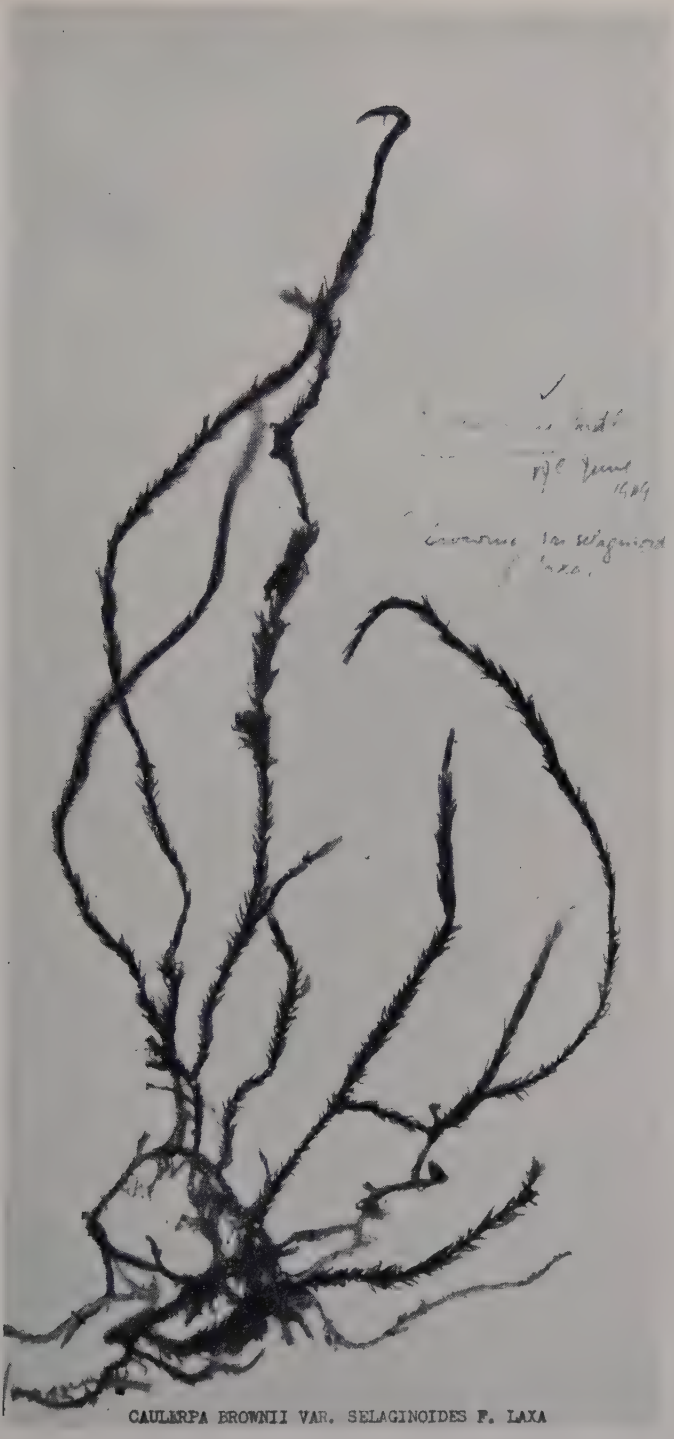
Top left: *Bryopsis derbesioides* sp.nov. (× ⅔). Bottom left: *Bryopsis olivacea* sp.nov. (× ⅔).
Top right: *Bryopsis pseudoplumosa* sp.nov. (× ⅔). Bottom right: *Bryopsis tetrasticha* sp.nov. (× ⅔).



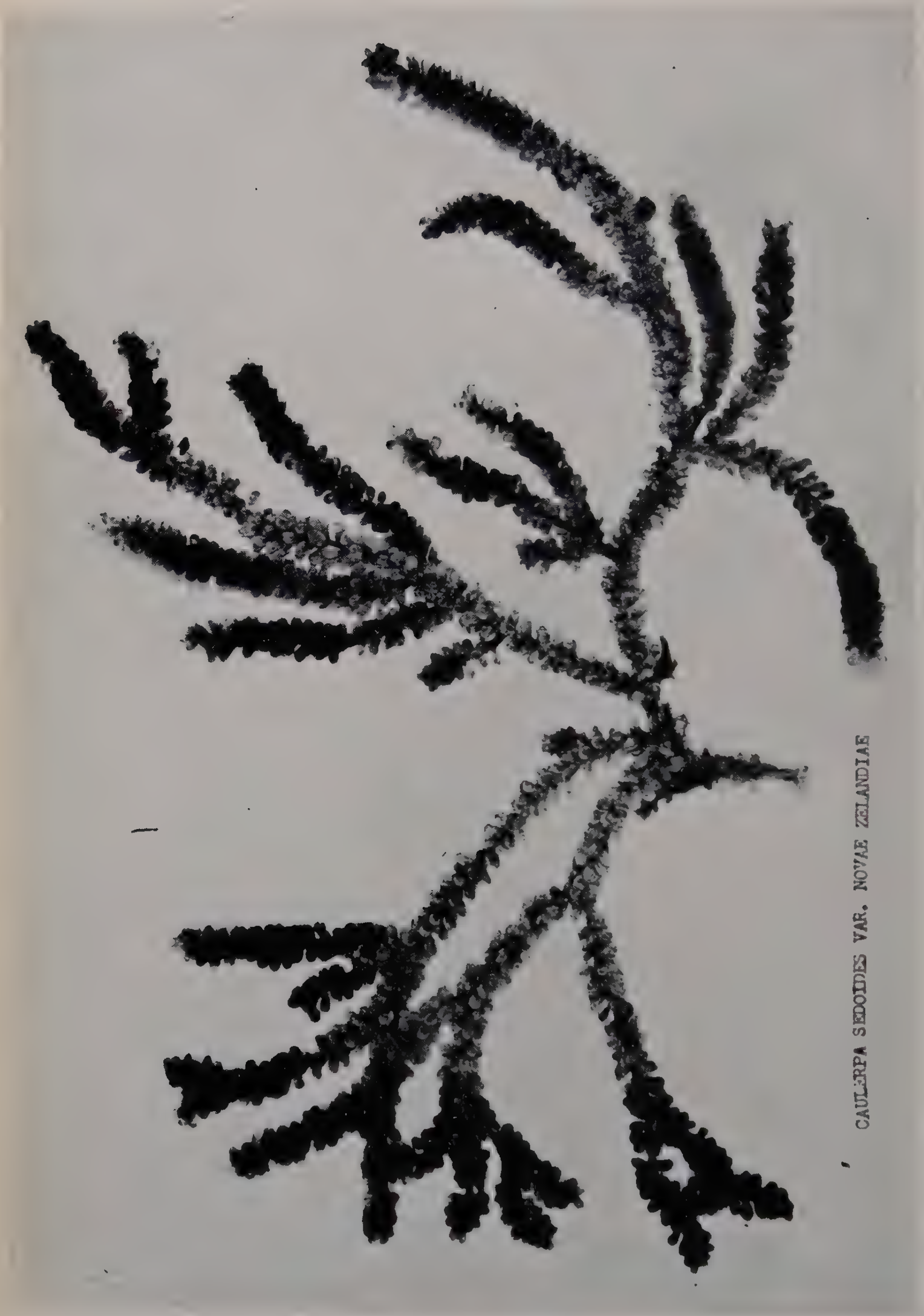
Right: *Bryopsis pseudopennata* sp.nov. ($\times\frac{2}{3}$). Top left: *Bryopsis corticulans* Gardn. var. *novae-zelandiae* var.nov. ($\times\frac{2}{3}$). Bottom left: *Bryopsis fusca* sp.nov. ($\times\frac{2}{3}$).


ALGAE NOVA ZELANDICAE EXSICCATAE
No 153
Kaikoura.
CAULERPA BROWNII ENDL. VAR SELAGINOIDES
HERBARIUM OF VICTOR W. LINDAUER
ALGAE NOVA ZELANDICAE EXSICCATAE
No 27
Bay of Islands

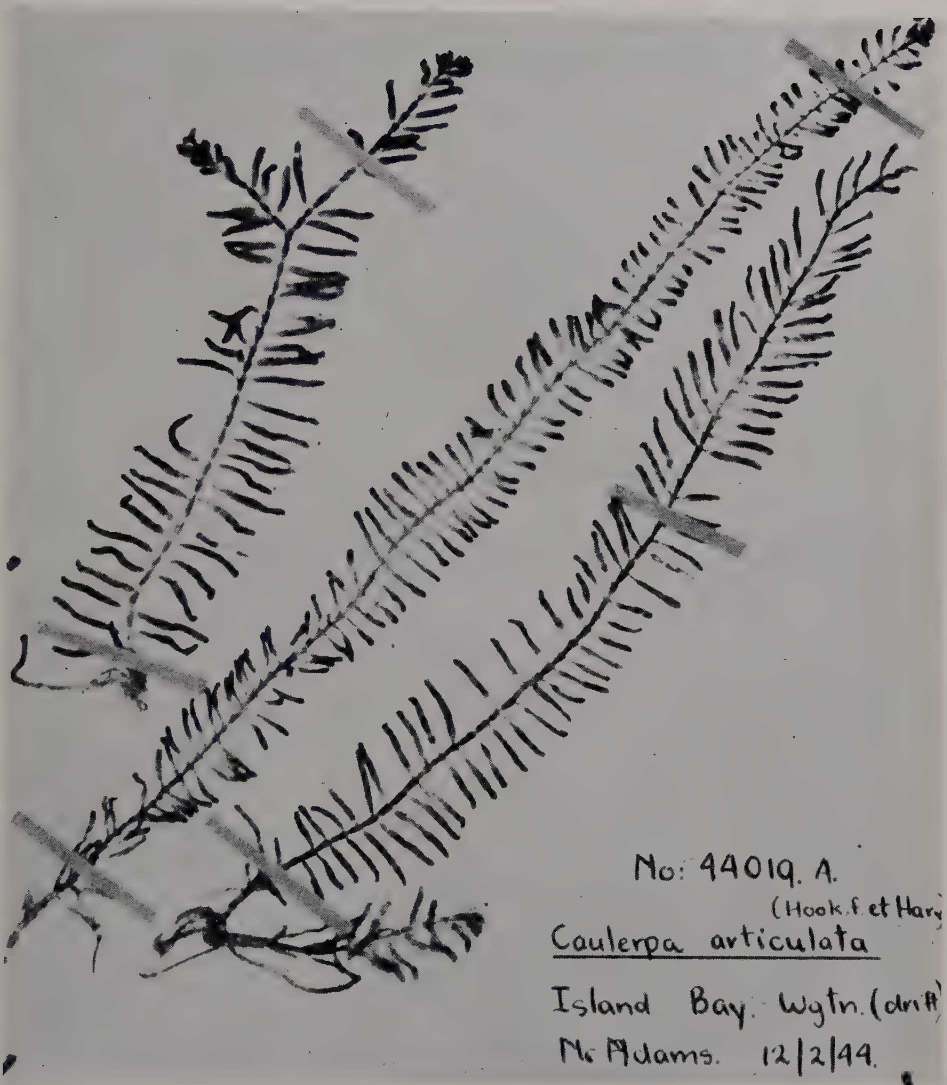
Top: *Caulerpa brownii* var. *selaginoides* J. Ag. (×½). Bottom: *Calerpa hypnoides* var. *flexilis* f. *novaezelandiae* Web. v. Bosse. (×½).



Caulerpa brownii var. *selaginoides* f. *laxa* form.nov. (× $\frac{2}{3}$).



Caulerpa sedoides f. *novaezelandiae* form.nov. (× $\frac{2}{3}$).



Caulerpa articulata Harv. (× $\frac{2}{3}$).

A New Genus of Meliaceae from Eastern Africa. By BERNARD VERDCOURT, Assistant Botanist, East African Herbarium, Nairobi.

(With 1 Text-figure)

[Read 21 April 1955]

About 45 years ago Sim (1909) described a tree from Portuguese East Africa which he referred to the genus *Bersama*, namely, *B. mossambicensis*. Whilst I was studying the genus *Bersama* (*Kew Bull.* 1950, pp. 233–44), it was at once evident that Sim's species was not only placed in the wrong genus but also in the wrong family. Nothing could be done at the time, other than to point out this fact, since only fruiting material was available. It seemed remarkable that this tree, which is frequent all down the African coast from Kenya to Zululand, had never been collected in flower, or at least flowering material had never been associated with fruiting material. It is possible that flowering material will be found at Kew somewhere in the Meliaceae or Sapindaceae folders, since from the small inflorescence alone no one would place the plant in *Bersama*. The flowers are, however, very inconspicuous, unlike the large scarlet fruits, and it is perhaps not surprising that they have been overlooked. Mr E. Trump and Mr W. Langridge have recently obtained flowers in the Sokoke Forest, Coast Province, Kenya, and have enabled this account to be drawn up. My best thanks are due to these collectors for their assistance. The general appearance of the plant at once suggests Meliaceae, and Sim did in fact mention the close resemblance to *Trichilia*. He realized at the time of description that the tree was not a true *Bersama*, but unwilling to describe a new genus he placed it in the one it appeared most to resemble. He excluded the plant from the Meliaceae, stating that the filaments were not united. This mistake is understandable, since the union is poor and in male buds the filaments are almost free. The flowers he examined were not mature. The filaments in *Bersama* are in any case quite united at the base. There are several characters which entirely exclude the plant from *Bersama* and, indeed, from the Melianthaceae and Sapindaceae as a whole (I think that these two families are dubiously separable). The short, slender, few-flowered inflorescence is quite different from the robust racemes found in *Bersama*. The leaves are exstipulate and have a different venation. There are 12 stamens united into a tube instead of 4–5 poorly united or free; the disc is within the staminal ring and not angular and outside. The pollen grains show several differences. Points of resemblance are the hard woody 5-valved capsule and the presence of functionally male or female flowers similar to those found in *B. abyssinica* Fres. subsp. *abyssinica*. I believe that the best position for the plant is in the Meliaceae—Melioideae. Using the classification proposed in Engler and Prantl, *Die Natürliche Pflanzenfamilien*, it would be placed near to *Trichilia*. As mentioned above there is a quite close external resemblance to this genus, but the capsule is thick and woody and the ovary 5-celled in *B. mossambicensis*. The degree of connation of the filaments is very variable in *Trichilia*, being limited to the base in some species. The pollen is similar to that usually found in the family. The species cannot be accommodated in *Trichilia*—the fruits are too different in structure. The staminal tube also lacks the appendages usually found in that genus. A new genus is unfortunately necessary. It was thought very possible that flowering material of this species might have been redescribed under another name, but nothing has so far been found in the literature. A formal description of the new genus and an account of the species are given below. I am grateful to Miss E. M. Stones for preparing the accompanying figure.

Pseudobersama Verdcourt, gen.nov. (Meliaceae—Melioideae) a **Trichilia** ovario 5-loculari, fructu lignoso differt.

Arbor mediocris. *Folia* alterna, exstipulata, imparipinnata, foliolis alternis vel ± oppositis, 4–7-jugis, integerrimis, acuminatis. *Inflorescentiae* pauciflorae, cymosae, breviter pedunculatae, bracteae parvae, ex axillis foliorum solitariae exorientes. *Flores* polygami, hypogyni, actinomorphi, parvi. *Calyx* brevis urceolatus 5-fidus, lobis deltoideis ± acutis, alabastro apertis. *Petala* 5, oblonga, libera, apice obtusa, basi angusta, alabastro imbricata. *Discus* annularis, angustus, 0·5 mm. altus, cum ovario basi concretus. *Flores* ♂: *Stamina* 11–12, filamentis basi connatis. *Antherae* hirsutae, oblongae, dorsifixae, biloculares, loculis longitudinaliter et lateraliter dehiscentibus. *Ovarii rudimentum* cylindricum hirsutum. *Flores* ♀: *Stamina* infertilia 12, filamentis basi connatis disci extra insertis, antherodiis hirsutis. *Ovarium* ovato-globosum, dense hirsutum, 5-loculare, in stylum attenuatum, stigmate capitato leviter 4–5-lobato, ovula in loculis 2, superposita, anatropa, micropyle supera, angulo centrali affixa. *Capsula* valde lignosa, extra echinata, loculicide 5-valvis, loculis 1–2-spermis. *Semina* arillo rubro carnoso inserta; testa nitida, radicula supera; albumine nullo.

Species unicum: *Pseudobersama mossambicensis* (Sim) Verdcourt in Africa Orientali Tropicali endemicum.

Dr Erdtman has kindly commented on a sample of pollen from the new genus and gives the following diagnosis (*in litt.*). Pollen grains *4-colporate*, subprolate (37–31μ), sexine *as thick as nexine* or *thinner*, without distinct pattern. Ora crassimarginate, *slightly* lalongate. They differ from the grains found in the Melianthaceae in the characters in italics. The pollen grains are quite similar to those of some Sapotaceae with which family the genus has no affinity. The above pollen description does not exclude the genus from the Meliaceae in any way.

Pseudobersama mossambicensis (Sim) Verdcourt comb.nov.

Bersama mossambicensis Sim, *Forest Flora of Port. E. Africa*, 34, t. 23 (1909).

Tree to 30 ft., probably growing larger ('sometimes a very large tree', Sim). Branchlets grey below, young parts reddish or orange-brown, ridged, minutely pubescent; upper internodes 1–2 cm. long. Very young leaves densely velvety pubescent, adult leaves glabrous save for the basal part of the rachis. *Leaves* exstipulate imparipinnate, 15–50 cm. long, petiole up to 10 cm. long, thickened at the base, more or less terete, finely pubescent or glabrescent. *Leaflets* 9–15, alternate or subopposite, elliptic or oblong-elliptic, cuneate at the base, more or less unequal, acuminate at the apex, acumen rounded or minutely emarginate, 8 × 3·3 to 17 × 5·5 cm., lateral nerves 5–12, arcuate and recurving near the edge, venation openly reticulate, prominent below; petiolules 4–15 mm. long. *Flowers* 3–11 in lax to subcapitate compound cymose inflorescences, each part of the inflorescence bearing a simple 3-flowered cyme, peduncle 0·5–2 cm. long, bracts minute pubescent 1–1·5 mm. long, bracteoles minute, pedicels 0·5–1 mm. long. The flowers are functionally either male or female. Whether both kinds occur on one plant or not is at present uncertain. *Male flowers*: about 7 mm. long. *Calyx* rather thick and fleshy, papillate, tube 2 mm. long divided into 5 short bluntly triangular lobes. *Petals* 5, oblong, 5 mm. long and 2 mm. wide. *Stamens* 11–12 united into a tube 2 mm. long at the base, filaments about 3·5 mm. long and anthers 1 mm. long, hairy, dehiscing laterally by longitudinal slits. In very young buds and old flowers the cohesion of the filaments is less prominent, which probably explains Sim's statement. *Rudimentary ovary* cylindrical, densely hairy. *Female flowers*: *Calyx* urceolate, 3·5 mm. long, lobes 5, triangular, thick, 2 mm. long and broad, rugulose and slightly pubescent outside, glabrous and shining inside; aestivation open. *Petals* oblong 5·5 mm. long and 2 mm. wide, obtuse at the apex,

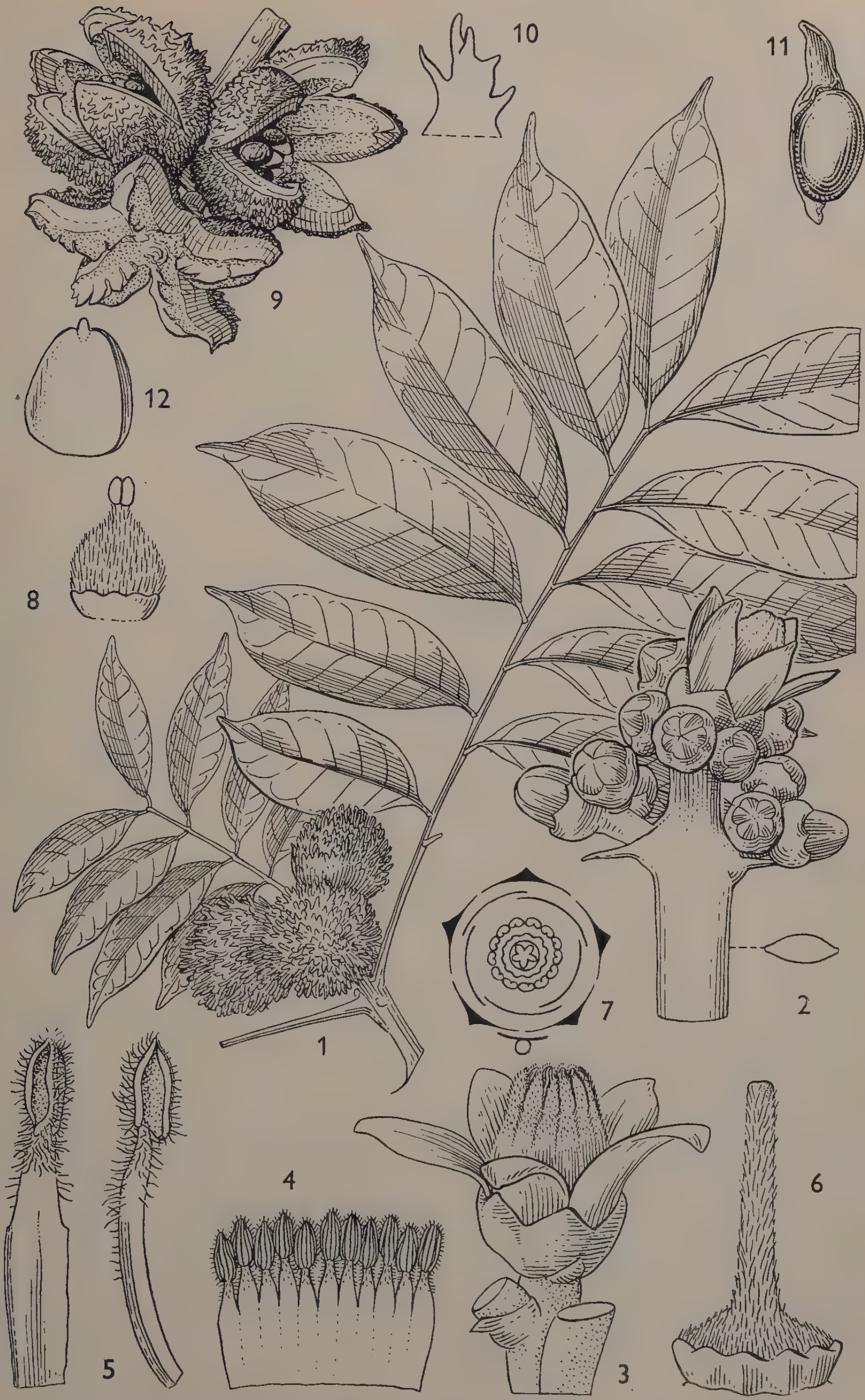


Fig. 1. 1, twig showing immature fruit, × $\frac{1}{2}$. 2, male inflorescence, × 3. 3, male flower, × 6. 4, staminal tube, opened out, from within, × 6. 5, stamens, × 12. 6, rudimentary ovary from male flower, × 12. 7, floral diagram of female flower. 8, ovary, from a drawing by Verdcourt, × 4. 9, infructescence, × $\frac{2}{3}$. 10, appendage from surface of capsule, × 4. 11, seed, with aril, × 2. 12, cotyledons, × 4. 1 and 9–12 from Drummond & Hemsley 3957; 2–7 from Langridge (in spirit); 8 from Trump (in spirit).

narrowed to the base where they are 1·5 mm. wide, minutely granular outside and inside along lines of overlap, with a slight longitudinal median keel. *Filaments* 12 united below for 2–3 mm., glabrous, above free and hairy for about 1·5 mm. Anthers about 1 mm. long, sterile, with long shaggy hairs. *Ovary* globose 3 mm. in diameter and 2·5 mm. long, densely hairy, apically attenuated into a style 1 mm. long, stigma globose, vaguely 4–5-lobed, 0·7 mm. long, stigmatic surface at middle of apex. Ovary 5-locular, ovules 2 in each cell superposed, attached to the central axis. *Fruit* a very woody capsule 3–4·5 cm. in diameter densely covered with lobed antler-shaped appendages 7 mm. long. Capsule dehiscing loculicidally from the apex into 5 valves which do not separate completely, walls of valves 5 mm. thick and fruit stipe about 5 mm. long. *Seeds* 2 in each cell, subglobose, but somewhat triangular in outline, the area facing the base of the fruit rather flat, the opposite end bluntly pointed, 6 × 7 × 4 mm. Testa leathery, shiny and red purple outside, inner layer crustaceous or slightly woody, raphe 7 mm. long. Aril only covering a small part of the ventral surface of the seed. Radicle superior. The cotyledons are enclosed in a thin coating which has a brownish basal patch. Cotyledons thick, flat and fleshy, 5 mm. long, 4 mm. wide and 1·5 mm. thick.

DISTRIBUTION

KENYA. Coast Province, Sokoke Forest near Kilifi, on red sandy loam at junction of *Mimusops-Afzelia* and *Brachystegia* zones of forest, May 1954, *Langridge* s.n. (EA.); ditto, 120 m., 14 April 1954, *Trump* 141 (EA., K.): tree to 6 m., flowers small, greenish white, fruits scarlet, 'mtuma-mcherere' (vern.); ditto, 60 m., 2 August 1937, *Moggridge* 430 (EA., K.), 'muzeri-zeri' (vern.); ditto, 60 m., July 1936, *Moggridge* 120 (EA., K.). Kwale District: Buda Mafisini Forest, 8 miles west-south-west of Gazi, 80 m., in secondary tree-layer of coastal forest, 22 August 1953, *Drummond & Hemsley* 3957 (K.): small tree, 10 m., in fruit only; fruits red. Shimba Hills, 300 m., May 1930, *G. H. Donald* 33 in FD. 404 (EA., FHO.): medium-sized tree, fruit large, bright scarlet with honeycombed surface, 'mlala-iku' (kiswah.). Gogoni Forest, *Graham* 1671 (EA., K.): tree with red seeds, 'mlalaiku' (kiswah.). Shimba Hills, November 1931, *Mac Naughton* 513 (EA.): tree to 9 m., fruit large fleshy (*sic*) eaten by birds, grows in undergrowth of high forest, poles used for native hut-building, 'mlala-iku' (kiswah.). Galla country, without locality, 1880, *Wakefield* s.n. (K.).

TANGANYIKA. Pungutini, Kipata, coast, 5 April 1912, *Braun* 3688 (EA.). Kiserawe District, Kisiju, Kerekese Forest Reserve, September 1953, *Paulo* 154 (EA., K.): tall slender tree; fruits red. Ditto, fairly common, September 1953, *Semsei* 1387 (EA., K.): fruits red. Kiserawe District, Pugu Forest Reserve, June 1954, *Semsei* 1762 (K, EA): slender tree with red fruits.

PORTUGUESE EAST AFRICA, sine loc., 'frequent', *Sim* 5204 (holo., ubi) (there is no doubt attached to the identification of Sim's plant so I have not persevered in my search for the type; the collection was divided between numerous herbaria and it does not exist in any of those I have written to in inquiry). Manica and Sofala, Cheringome Chiniziua in *Brachystegia spiciformis*, *Millettia*, *Afzelia* woodland, October 1949, *Pedro* and *Pedrogão* 8863 (PRE.); tree 6–8 m. tall. Mile 10 on the Trans Zambesi Railway, July 1922, *Honey* 711 (K., PRE.): large evergreen tree in thick forest and open bush, timber very durable and light, 'garamagibu' (vern.). Santaca, region of Maputo, south of Lourenço Marques, 16 September 1948, *Gomes Sousa* 3841 (PRE.): shrub 3–4 m. tall with red fruits, common in open forest on sandy soil, fruit in April.

SOUTH AFRICA, ZULULAND. Mangusi Forest, July 1923, *Boocock* 16 in FD. 5313 (PRE.): tree 15 cm. in diam. and 9 m. tall; same locality, 19 May 1939, *H. H. Curson* s.n. (K., PRE., EA.).

Cytotaxonomic studies on the Gold Coast species of the genus Commelina Linn.

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(With Text-figures 1–28)

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Preliminary observations on the genus *Commelina* made during 1951 and 1952 indicated the presence of a number of unrecorded and also several apparently undescribed species in the Gold Coast. The abundant variation of several species, in particular *C. gerrardi* and *C. diffusa*, suggested that they were not homogeneous, whilst examination of many of the type specimens indicated some duplicity of names. Subsequent work on the genus has largely confirmed these observations and is described in the present paper.

Material was collected from most regions of the Gold Coast and introduced into cultivation in the Botanic Gardens of the University College of the Gold Coast at Achimota, where it was grown under standardized optimum conditions of partial shade and adequate water supply. In addition, several species were grown fully exposed to the sun and with a reduced water supply. By these means it was possible to confirm the effects of certain environmental influences and produce variations in the plants similar to those observed in the field.

Variation. The species and variants of *Commelina* described in this paper show little variation when grown under cultivation. However, in the field the effects of environment produce a wider range of variation which, in several cases, has been regarded as specifically and even sectionally distinct. Transplant and other experiments in which water supply and exposure have been varied show that the following characters are frequently affected by the environment: length of internode, presence of purple pigment in the stem and leaf-sheath, density of pubescence, length of leaf in relation to breadth, number of spathes borne together (in species where there is a tendency for the spathes to occur in groups) and to a very limited degree the shape of the spathes, in which the length of the acumen may vary. The occurrence of capsules in which one or more of the ovules or loculi have failed to develop is very common. This appears to be fortuitous and is not noticeably affected by the environment. Characters which vary but little with the environment include habit, type of pubescence (i.e. length, colour and shape of the hairs), general leaf shape, spathe characters, floral characters including colour, development of the lower petal and the shape of the sterile anthers of the staminodes, and the characters of fully matured seeds. Mature seeds, when available, provide one of the most useful diagnostic characters in this genus, but they are produced in small numbers and are usually shed as soon as they reach maturity. Hence they are frequently not available in herbarium material and may even be difficult to obtain in the field. Seeds only attain their final characters within a few hours of maturity, and then it is usual for them to be dispersed immediately. For this reason seeds dissected from capsules on herbarium material do not always show their mature characters and should be used with caution. Each species and subspecies described in this paper has a characteristic appearance when growing and can usually be recognized at a glance. Unfortunately herbarium material, in which such characters as habit, flower colour and structure are frequently lost, is not always so easy to identify.

Cytology. Chromosome counts were obtained from root-tip preparations, using a squash technique. Mitoses were found to be most abundant in the early morning. In order to shorten the chromosomes and so facilitate counting, root-tips were prefixed in a saturated aqueous solution of paradichlorobenzene for 1 hr. prior to fixation in 1:3 acetic alcohol. Fixed material was hydrolysed in normal hydrochloric acid at 58° C. for about 12 min. and squashed in aceto-carmine. Figs. 1, 2 and 3 are camera-lucida drawings of such preparations.

The diploid chromosome numbers of the Gold Coast species of *Commelina* are summarized in the table below:

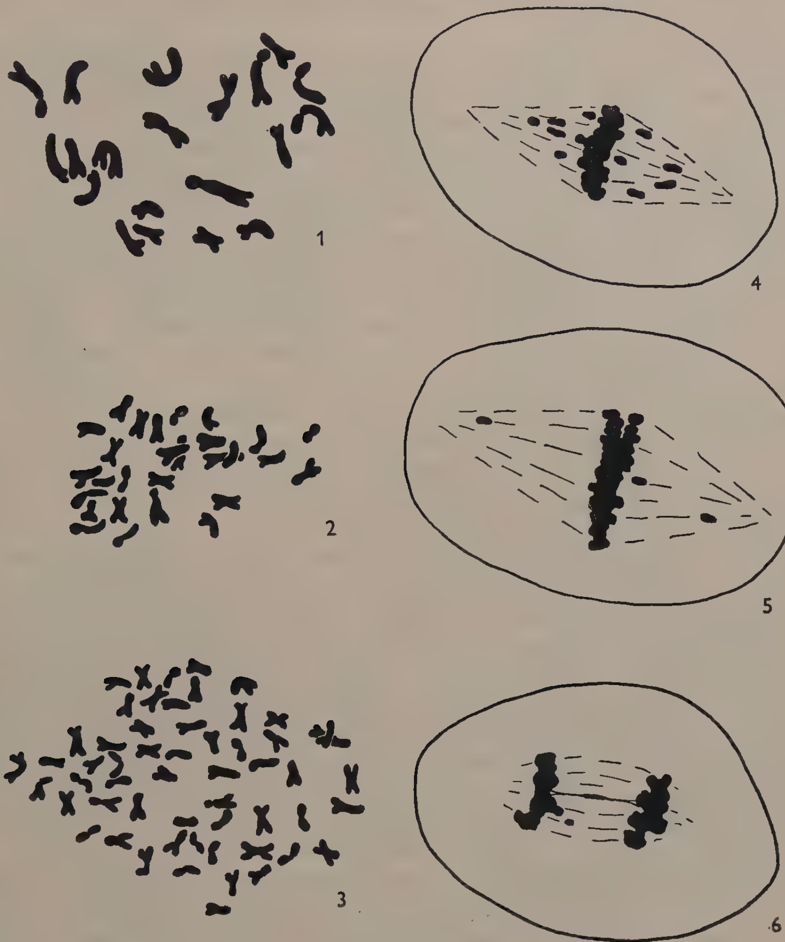
Species	$2n$
Commelina africana var. *africana*	28
C. africana var. *krebsiana*	28
C. aquatica	28
C. ascendens	28
C. aspera	28
C. benghalensis	28, 56
C. capitata	42
C. congesta	28
C. diffusa	28
C. forskalaei	28
C. gerrardi ssp. *gerrardi*	56
C. gerrardi ssp. *maritima*	56
C. lagosensis	28
C. livingstoni	56
C. macrospatha	28
C. macrosperma	20
C. thomasii	56
C. umbellata var. *umbellata*	28
C. umbellata var. *gambiae*	28

From these numbers it is clear that the genus contains a euploid series with a base number of 7. There also appear to be several species with a base number of 5. Besides *C. macrosperma*, which has a diploid number of 20, *C. diffusa* (under *C. nudiflora*) is reported as having a diploid number of 30 in West Indian material (Simmonds, 1954), and Anderson & Sax (1936) report a diploid number of 90 in *C. coelestis* Willd. The base number of 5 may have been derived from plants with 7 as the base number, either by loss of chromosomes or in some cases by fragmentation. The probable occurrence of fragments in *C. benghalensis* is noted by Anderson & Sax (1936).

It is clear that polyploidy has played little part in the recent evolution of the species of *Commelina* under consideration in this paper. Only in *C. benghalensis* do we find that polyploid differences exist between closely allied taxa. Thus *C. benghalensis* occurs in both a diploid and a tetraploid race which are taxonomically distinguishable and ecologically separated. They may be regarded as incipient species, for they have apparently also achieved genetical isolation. No intermediate plants have been observed in the field, even though in one locality both races have been found growing in close proximity. Also attempts to produce hybrids artificially have so far met with no success. This genetical isolation is probably largely to be attributed to the numerical differences between the genomes of the two plants rather than to any lack of homology between the individual chromosomes.

It is worthy of note that *C. benghalensis* is a plant with distinct weedy tendencies and is very widely distributed, being by no means confined to Africa. The only other comparable species under consideration in this paper is *C. diffusa*, which is a widespread weed in the warmer parts of the world. Its diploid chromosome number, in the several varied strains which we have examined from the Gold Coast, has always been 28, but, as previously noted, Simmonds (1954) reports a diploid number of 30 in West Indian material, whilst Anderson & Sax (1936) obtained a diploid number of 56 in the North American material examined by them. Whether these three plants are taxonomically distinct is not known, but this species is very variable and there is little doubt that a critical consideration of material from the whole of its range will reveal the need for subdivision.

The chromosome complements of the other closely allied taxa show no numerical differences. Both varieties of *C. umbellata* have a diploid number of 28; similarly, both subspecies of *C. gerrardi*, together with the closely allied and intercompatible *C. livingstoni*, have a diploid number of 56. Also *C. aquatica* and the closely allied *C. diffusa* both have a diploid number of 28.



Figs. 1–6.

Fig. 1. Metaphase plate from root-tip squash preparation of *Commelina macrosperma* J. K. Morton ($2n=20$). × 1900. Fig. 2. Metaphase plate from root-tip squash preparation of *C. africana* Linn. ($2n=28$). × 1900. Fig. 3. Metaphase plate from root-tip squash preparation of *C. gerrardi* ssp. *gerrardi* C.B.Cl. ($2n=56$). × 1900. Fig. 4. Metaphase I in P.M.C. squash preparation showing an untidy plate and unpaired univalents in the hybrid between *C. aquatica* J. K. Morton and *C. thomasii* Hutch. × 1750. Fig. 5. Metaphase I in P.M.C. squash preparation showing odd unpaired univalents in the hybrid between *C. livingstoni* C.B.Cl. and *C. gerrardi* C.B.Cl. × 1750. Fig. 6. Anaphase I in P.M.C. squash preparation showing a bridge and fragment structure in the hybrid between *C. gerrardi* ssp. *gerrardi* C.B.Cl. and ssp. *maritima* J. K. Morton. × 1750.

The position in the less closely allied species is rather different. Here there are clear polyploid differences between neighbouring species or groups of species. Thus *C. thomasii* is undoubtedly allied to *C. diffusa* but has a diploid number of 56. Again there are clear affinities between *C. gerrardi*, *C. lagosensis* and *C. congesta*, but the former has a diploid number of 56 while both the latter have 28. The remaining species, *C. capitate*, *C. macro-*

spatha, *C. macrosperma*, *C. ascendens*, *C. africana*, *C. aspera* and *C. forskalaei*, differ widely both from each other and from the species already considered, and in these there is a greater divergence of chromosome number, with diploid numbers of 20, 28 and 42. The chromosome numbers of *C. macrosperma* and *C. capitata* ($2n = 20$ and 42 respectively) suggest a possible hybrid ancestry, but these two species differ so considerably from the other Commelinas in this part of Africa that there is at the moment no clear indication of their ancestry.

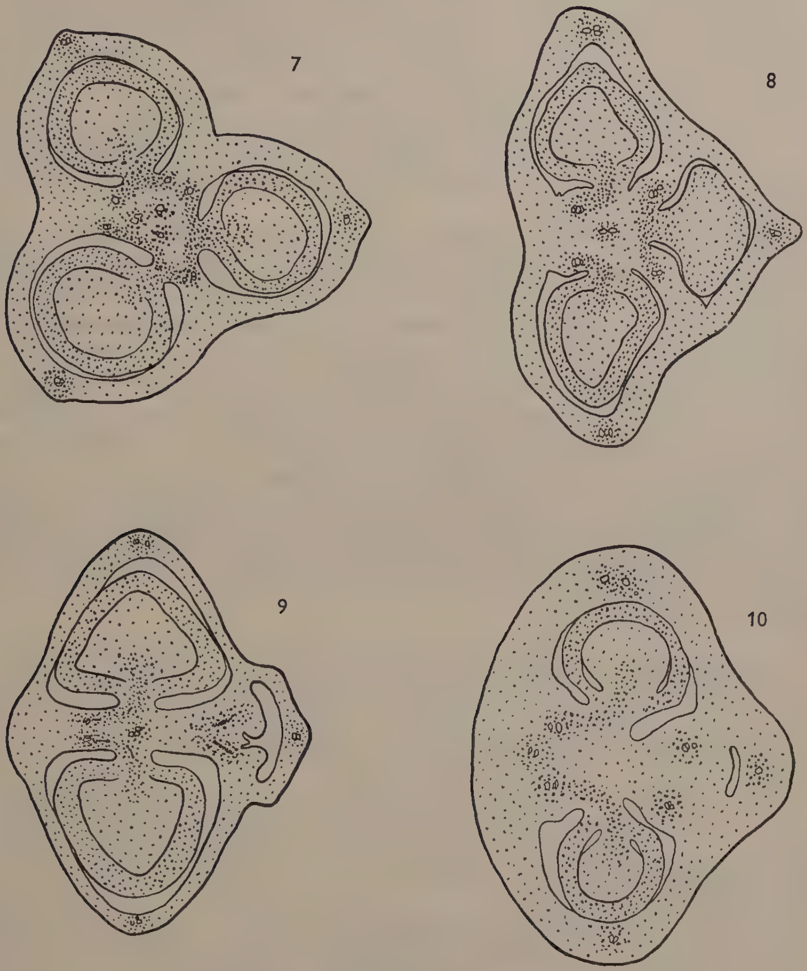
Meiosis was studied in pollen mother cells after fixation in 1:3 acetic alcohol and squashing in aceto-carmine. Meiosis proceeds normally in the several species which have been examined. A cell wall is laid down after each division of the pollen mother cell nucleus. Several naturally occurring hybrids have been examined, and these have shown various irregularities during meiosis. They include the following:

C. livingstoni × *C. gerrardi*. Plants of this parentage occur quite frequently in the Gold Coast at the southern edge of the range of *C. livingstoni* where *C. gerrardi* usually abounds. They are intermediate between the parents and set fertile seed despite the frequent occurrence of minor irregularities during meiosis. Pairing of the chromosomes is high, but commonly one or more univalents do not take up their positions on the metaphase plate (Fig. 5). Tetrad and gamete formation appear to be almost normal. Exsicc. Morton A685 (G.C., B.M.).

C. gerrardi ssp. *gerrardi* × ssp. *maritima*. Plants of this parentage are abundant along the coast in the east of the country where the two subspecies frequently grow together. They are fertile, and gamete formation has been normal in the plants examined, though frequently bridge and fragment structures occur at metaphase I (Fig. 6). Exsicc. Morton A828 (G.C., B.M.) and A171 (G.C., B.M.).

C. aquatica × *C. thomasii*. A large colony of plants referable to this hybrid was discovered growing near the parents in open marshy ground in forest country south of Kade. The plants were intermediate in appearance between the parents, but in herbarium material they are difficult to separate from the former parent. They produced very few flowers and these were completely sterile. A full investigation of meiosis was impossible in the small amount of flowering material available, but a pollen mother cell preparation showing first meiotic metaphase had an untidy plate with many unpaired univalents (Fig. 4). Heterosis was most pronounced, and the plants straggled for many metres and produced numerous erect non-flowering shoots. Grown under cultivation for the past two years these plants have failed to flower, but have produced considerable quantities of straggling vegetative growth. Exsicc. Morton CG8350 (B.M., G.C.).

Classification. The production of a satisfactory system of classification in the genus *Commelina* is far from simple. C. B. Clarke (1881) produced a system based on ovary and capsule characters, primarily dividing the genus on the basis of the number of ovules in the ventral loculus of the ovary, and secondarily on the development and dehiscence of the dorsal loculus of the capsule. This primary division into subgenera *Didymoon* and *Monoon* is clear-cut, at least in the species under consideration here, though it separates the closely related *C. umbellata* and *C. gambiae* which are regarded by the writer as minor variations of the same species. The division of the subgenus *Didymoon* into sections *Eu-Commelina*, *Heterocarpus* and *Dissecocarpus* is less satisfactory. In particular, we are unable to separate reliably the first two of these sections, which are supposed to differ in having the dorsal loculus of the capsule eventually dehiscent or indehiscent. Undoubtedly some species can be separated by this means, e.g. *C. benghalensis* apparently always has this loculus dehiscent and *C. africana* always indehiscent, but other species are intermediate, e.g. *C. congesta*, *C. diffusa* and *C. thomasii*, and show variation from capsule to capsule. Hence, in the classification given below we have united the sections *Eu-Commelina* and *Heterocarpus* while still retaining the section *Dissecocarpus* which appears to be a reasonably distinct group. The division *Monoon* has been similarly treated and the sections *Trithyrocarpus* and *Heteropyxis* are regarded as indistinguishable. The very common *C. gerrardi* provides an example of this, for the third loculus of its ovary may dehisce as readily as the others or less readily, or may on occasions be completely indehiscent, though the plants show no other differences. The section *Spathodithyros* is a reasonably distinct group and is therefore retained.



Figs. 7–10.

Fig. 7. Transverse section of the ovary of *C. umbellata* var. *umbellata* Thonn. × 100. Fig. 8. Transverse section of the ovary of *C. capitata* Benth. × 50. Fig. 9. Transverse section of the ovary of *C. livingstoni* C.B.Cl. × 62. Fig. 10. Transverse section of the ovary of *C. macrospatha* Gilg. and Lederm. × 100.

Though we have retained the division of the subgenera into sections on the basis of the development or abortion of the third loculus of the ovary, this character is subject to much variation and can only be reliably determined when adequate material is available. Very frequently plants which normally have a capsule with three loculi may bear capsules in which one or more of the loculi have aborted. This can make the identification of single herbarium specimens very difficult and has probably led to several species being placed in the wrong section of the genus. Thus we are unable to distinguish between *C. guineensis* Hua, *C. vogelii* C. B. Clarke, *C. aethiopica* C. B. Clarke and *C. gerrardi*

C. B. Clarke, and regard them as belonging to one and the same species, though they are placed by Clarke (in Thiselton-Dyer, 1901) into the sections *Trithyrocarpus*, *Heteropyxis* and *Spathodithyros* on the basis of the herbarium material available at that time.

The number of fully formed loculi present in the ovary at the time of flowering provides a better basis for classification than the number which may develop in the capsule. Figs. 7, 8, 9 and 10 show sections made at the time of flowering through the ovaries of four species of *Commelina*. In *C. umbellata* var. *umbellata* (Fig. 7) all three cells are equally well developed though frequently one or more may be abortive in the mature capsule. In *C. capitata* (Fig. 8) the ovule in the dorsal loculus of the ovary is a little smaller than the others and not completely formed. It apparently never develops into a seed. In *C. livingstoni* (Fig. 9) and *C. macrospatha* (Fig. 10) the dorsal loculus of the ovary is rudimentary at the time of flowering, though the remains of the loculus and the vascular strands are still present.

The division of the genus into sections on the basis of the development of the dorsal loculus of the ovary cannot be taken as an indication of phylogenetic relationship. Thus *C. livingstoni* and *C. gerrardi* belong to different sections of the subgenus *Monoon*, but they are interfertile and hybrid populations frequently occur. An examination of meiosis in these hybrids has shown that the incompatability between the parental chromosome sets is slight and morphologically the two species show many similarities. Hence it is reasonable to conclude that the two species are closely related despite their being placed in different sections of the genus. Similarly, the two varieties of *C. umbellata* are clearly closely related, but they belong to different subgenera.

A key for the identification of the Gold Coast species of the genus *Commelina* based on capsule characters is provided, but because of the difficulties frequently encountered in using these characters an alternative key, which as far as possible omits capsule characters, has been produced with the object of providing a more ready means of identifying these plants.

A key to the Gold Coast species of Commelina *(based on capsule characters)*

1. Ovules 2 in each ventral loculus of the ovary (Didymoon). **2**
Ovules 1 in each ventral loculus of the ovary (Monoon). **12**

2. Ovary with dorsal loculus fully developed (Eu-Commelina and Heterocarpus). **3**
Ovary with dorsal loculus rudimentary or smaller and abortive (Dissecocarpus). **10**

3. Margin of spathe fused. **4**
Margin of spathe not fused. **6**

4. Plant scandent, younger parts with hooked hairs, spathes twice as long as broad, borne on a short leafless branch bearing scaly leaf sheaths. *ascendens*
Plant not as above. **5**

5. Seeds smooth, leaves small ovate-elliptic. *forskalaei*
Smooth reticulate, leaves large ovate-lanceolate. *benghalensis*

6. Seeds smooth. **7**
Seeds reticulate. **8**

7. Flower yellow, spathe medium to small. *africana*
Flower pale violet (almost white) spathe very large. *thomasii*

8. Plant covered with hooked hairs in younger parts, spathes not acuminate. *ascendens*
Plant glabrous or with straight hairs, spathes acuminate. **9**

9. Flower large blue, upper petals with long claw, flowering branches erect, leaves exceeding 5 times as long as broad. *aquatica*
Flower small violet, upper petals with short claw, branches creeping, leaves usually less than 5 times as long as broad. *diffusa*

10. Spathe elongate, margins not fused. *macrospatha*
Spathe not elongate, margin at least slightly fused at the base. 11

11. Plant large, seeds almost white, leaves ovate-lanceolate. *capitata*
Plant small, seeds brown, leaves linear. *umbellata* var. *gambiae*

12. Ovary with dorsal loculus developed (Trithyrocarpus and Heteropyxis. 13
Ovary with dorsal loculus rudimentary or small and abortive (Spathodithyros) 18

13. Leaves linear more than 8 times as long as broad, plant small. 14
Leaves lanceolate to ovate-lanceolate less than 6 times as long as broad, plant medium to large. 15

14. Spathes clustered, plant erect not rooting at the nodes. *aspera*
Spathes borne singly, plant straggling and rooting at the nodes. *umbellata* var. *umbellata*

15. Flower very pale violet (almost white), spathes sessile broadly triangular, hardly oblique. *congesta*
Flower bright blue or violet, spathes shortly stalked ovate triangular, very oblique. 16

16. Leaves lanceolate exceeding 4 times as long as broad, spathe acute, plant straggling or erect. *gerrardi* ssp. *gerrardi*
Leaves ovate-lanceolate less than 4 times as long as broad, spathes obtuse, plant creeping. 17

17. Plant shortly pubescent, not fleshy. *lagosensis*
Plant glabrous, fleshy, maritime. *gerrardi* ssp. *maritima*

18. Seed smooth with small thickened ridges at either side, leaves lanceolate, flower blue. *livingstoni*
Seed coarsely reticulate without thickened ridges, leaves ovate, flower white. *macrosperma*

Key to the Gold Coast species of Commelina (*omitting capsule characters*)

1. Spathes with margins not fused. 2
Spathes with margins fused. 8

2. Flower yellow. 3
Flower blue, violet or white. 4

3. Spathes elongate longly acuminate, leaf narrowly lanceolate. *africana*
Spathes short (up to twice as long as broad) not acuminate, leaf ovate-lanceolate. *capitata*

4. Plant scandent, with hooked hairs, spathes not acuminate. *ascendens*
Plant erect or straggling, hairs not hooked, spathes longly acuminate. 5

5. Seeds smooth, flower very pale violet (almost white), a large straggling plant. *thomasii*
Seeds pitted or reticulate, flower bright blue or violet. 6

6. Seeds large pitted, covered with white powder, spathes elongate narrow, as broad in middle as at the base. *macrospatha*
Seeds small reticulate dark brown to black, spathes longly acuminate, much broader at base than in middle. 7

7. Flower large pure blue, claw of upper petals long, leaves narrowly lanceolate exceeding 5 times as long as broad, flowering branches erect. *aquatica*
Flower small violet, claw of upper petals short, leaves usually broadly lanceolate less than 4 times as long as broad, all branches creeping. *diffusa*

8. Seeds smooth. 9
Seeds wrinkled, pitted or warted. 15

9. Spathes acute and acuminate (rarely obtuse in C. livingstoni). **10**
Spathes obtuse and not or hardly acuminate. **12**

10. Plant small compact, leaves linear, spathes crowded together. *aspera*
Plant large straggling or erect, leaves lanceolate, spathes usually single. **11**

11. Plant stout usually erect, seeds with 2 thickened lateral ridges, capsule large 2-celled with 2 ridges at the apex. *livingstoni*
Plant slender usually straggling, seeds not ridged, globose, capsule 3-celled without apical ridges. *gerrardi* ssp. *gerrardi*

12. Spathes broadly triangular hardly oblique sessile and terminal, flower pale violet (almost white). *congesta*
Spathes ovate very oblique, shortly stalked, terminal and lateral, flower blue. **13**

13. Plant producing underground fruits, first flowers exserted on long persistent pedicels, seeds elongate. *forskalaei*
Plant without underground fruits, all pedicels included in spathe, seeds almost globose. **14**

14. Plant shortly pubescent not fleshy. *lagosensis*
Plant glabrous fleshy. *gerrardi* ssp. *maritima*

15. Leaves linear. **16**
Leaves lanceolate to ovate. **17**

16. Seeds reticulate, 2 in each ventral loculus of capsule. *umbellata* var. *gambiae*
Seeds with 2 pits and with small warts, 1 ovule in each ventral loculus of the ovary. *umbellata* var. *umbellata*

17. Plant scandent with hooked hairs. *ascendens*
Plant erect or straggling, hairs (if present) not hooked **18**

18. Flower yellow, plant erect stout, seeds pitted. *capitata*
Flower not yellow, plant straggling, seeds reticulate. **19**

19. Plant glabrous, flower white, seeds large. *macrosperma*
Plant pubescent, flower violet, seeds small. *benghalensis*

Classification of the Gold Coast species of the genus Commelina *Linn.*

Subgenus *Didymoon*. Ovules 2 in each ventral loculus of the ovary.

Section A (Eu-Commelina and Heterocarpus). Ovary with dorsal loculus fully developed.

- *C. ascendens* J. K. Morton
- *C. forskalaei* Vahl
- *C. benghalensis* Linn.
- *C. africana* Linn.
- *C. thomasii* Hutch.
- *C. aquatica* J. K. Morton
- *C. diffusa* Burm. f.

Section B (Dissecocarpus). Ovary with dorsal loculus rudimentary or reduced and abortive.

- *C. macrospatha* Gilg & Lederm.
- *C. capitata* Benth.
- *C. umbellata* var. *gambiae* (C.B.Cl.) J. K. Morton

Subgenus *Monoon*. Ovules 1 in each ventral loculus of the ovary.

Section C (Trithyrocarpus and Heteropyxis). Ovary with dorsal loculus fully developed.

- *C. aspera* Benth.
- *C. umbellata* var. *umbellata* Thonn.
- *C. congesta* C.B.Cl.
- *C. gerrardi* C.B.Cl.
- *C. lagosensis* C.B.Cl.

Section D (Spathodithyros). Ovary with dorsal loculus rudimentary or reduced and abortive.

- *C. livingstoni* C.B.Cl.
- *C. macrosperma* J. K. Morton.

DESCRIPTIONS OF THE SPECIES

Commelina africana Linn. *Sp. Pl.* ed. i, p. 41 (1753); ed. ii, p. 60 (1762).

C. krebsiana Kunth, *Enum.* **4**, 40 (1843).
C. africana var. *krebsiana* C.B.C. in DC. *Monogr. Phan.* **3**, 164 (1881).

A straggling perennial *herb* rooting at the nodes. Indumentum variable, ranging from almost completely glabrous in plants growing in wet shady situations to densely hairy (=*C. krebsiana* Kunth) in plants growing in exposed places. *Leaf* sheath glabrous or pubescent with long pale brown hairs; lamina lanceolate *c.* 60 × 15 mm. with undulate margins. *Spathes* borne singly in the upper internodes on spreading peduncles which exceed half the length of the spathes, elongate *c.* 27 × 8 mm. without mucilage and with a long acumen and free margins. *Flowers* medium-sized *c.* 12 mm. diam., first flowers male and longly pedicellate, later ones hermaphrodite and shortly pedicellate. *Petals* bright yellow, the upper pair with a claw of medium length, the lower one small and ovate-triangular. *Anthers* 3 dark yellow on yellow filaments; infertile anthers of the staminodes 2, yellow, very small and elongate, with the upper and middle lobes obscure and the basal lobes elongate and parallel. *Capsule* elongate apiculate 3-locular, upper loculi dehiscent with 2 seeds in each, lower loculus indehiscent and single seeded. Subterranean abnormal capsules are sometimes produced. Seeds brown, smooth (microscopically reticulate). $2n = 28$ in both varieties.

Var. *africana* is subglabrous and has glossy green leaves and more elongate internodes. It grows in the forest areas.

Var. *krebsiana* C.B.Cl is densely pilose with colourless hairs and has shorter internodes, the stem being largely obscured by the leaf sheaths. It grows in thicket clumps on the coastal plains and in savannah transition areas.

Exsicc. Var. *africana*, Johnson 647 (G.C., K.); Morton GC 8308 (B.M., G.C.), GC 9327 (G.C.), GC 6316 (G.C.) and GC 8058 (B.M., G.C.).

Var. *krebsiana*, *Morton* A648 (B.M., G.C.), GC 8522 (G.C.), GC 8035 (G.C.), GC 9168 (G.C.) and GC 8487 (B.M., G.C.). Intermediate plants, Fishlock 116 (G.C.), Morton A788 (B.M., K., G.C.) and GC 8311 (G.C.).

Note. Plants belonging to this species usually retain their indumentum characters under cultivation. However, as there appear to be no other characters separating *C. krebsiana* and *C. africana* and as fertile intermediates frequently occur, these two plants are regarded by the writer as varieties of the same species.

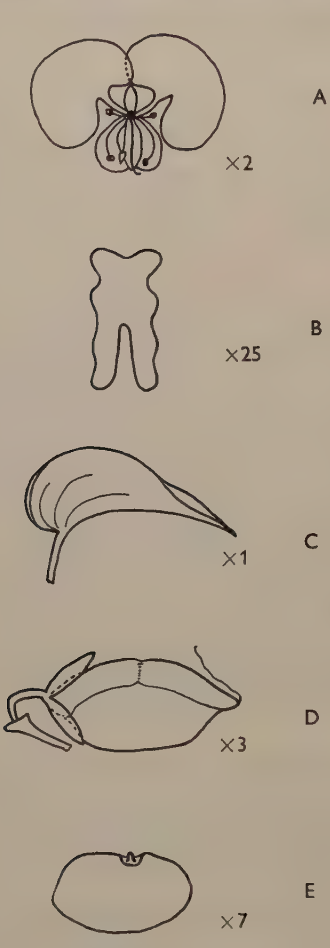
C. aquatica J. K. Morton sp.nov.

Herba gracilis et vaga, *C. diffusae* Burm. f. similis sed eo differens quod maior est elongationibusque ramis qui solum ex inferioribus nodis enascuntur et quod habet erectos florentesque ramos, angustiora folia, spathas plurumque maiores, flores maiores caerulei coloris splendidi ac puri superiora petala longo ungui, staminodium superioribus lobis mediae magnitudinis (parvis in *C. diffusa*).

Habitat. Circa aquam perennem in campis Accrensibus in Ora Aurea.

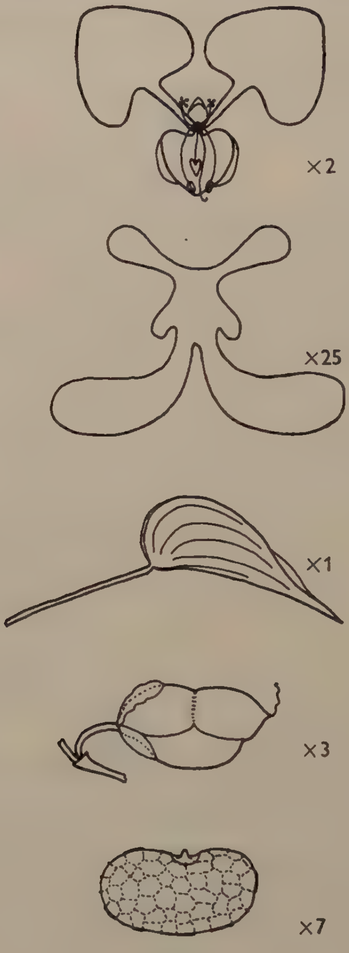
Typus. Morton A30 (B.M., G.C.).

A slender long-straggling perennial *herb* with erect branches rooting at the lower nodes. Indumentum variable usually glabrous apart from a few cilia on the edge of the leaf-sheath and petiole, rarely pubescent with colourless hairs. *Leaf* sheath long and slender, glabrous or pubescent; lamina narrowly lanceolate *c.* 60 × 10 mm. with thickened scabrid margins. *Spathes* borne singly in the axils of the upper leaves on long peduncles which frequently exceed the spathe in length, elongate (from 20 to 30 mm.), curved with a long acumen and free margins, without mucilage. *Flowers* large *c.* 15 mm. diam., first flowers male and very longly pedicellate, later ones hermaphrodite and shortly pedicellate. *Petals* retaining their rich cobalt blue colour when dried, the upper pair with a long claw, the basal one large cordate with a very short claw. *Anthers* 3 black with yellow pollen,



C. africana

Fig. 11.



C. aquatica

Fig. 12.

Figs. 11 to 28. A. Face view of a flower. B. Face view of an infertile anther of the staminode. C. Side view of a spathe. D. Capsule, side view in all except Figs. 13 and 15, which are ventral views. E. Seed.

the 2 outer ones with long colourless filaments, the inner one larger and with a shorter pale blue filament; infertile anthers of the staminodes 2 white with spreading lobes, upper lobes medium sized and yellow, middle lobes small and deflexed, lower lobes large and saccate. *Capsule* elongate apiculate 3-locular, the upper loculi dehiscent and each containing 2 seeds, the basal loculus single seeded and indehiscent. *Seeds* very dark grey with deep white reticulations. $2n = 28$ in both glabrous and hairy forms. A common plant around permanent standing water on the coastal plains.

Exsicc. Morton A30 (B.M., G.C.). Type: GC 8243 (G.C.), GC 8290 (G.C.) and GC 8075 (G.C.)—the glabrous form. A294 (B.M., G.C.), GC 8340 (G.C.) and GC 8501 (G.C.)—the hairy form.

Note. Hairy plants have not retained this character under cultivation.

When living this species is readily distinguished from *C. diffusa* by the following characters: large flowers; petals pure blue (not violet) and with a much longer claw; shape of the infertile anthers of the staminodes; the longer pedicels of the male flowers; the larger and more elongate spathe; the much longer leaf which is considerably narrower in proportion to the length; and the erect growth of the flowering branches. Further, these two species grow in quite different habitats, *C. aquatica* being a perennial component of the stable vegetation of permanently wet places on the coastal plains, while *C. diffusa* is a weedy, usually annual component of the transitional vegetation of damp disturbed soils. Many of the characters which separate these two plants are however lost or obscured in herbarium material, hence it is desirable that this should be accompanied by flowers preserved in spirit together with accurate field notes.

C. ascendens J. K. Morton sp.nov.

Planta singularissima, eo distincta quod scandere solet, et habet indumentum capillorum ascendentium et aduncorum, spathas parvas (c. 22 × 9 mm.) et lunatas marginibus paene solutis (enascentes ex patulis inflorescentiis) in quibus una quaeque spatha folio subtenditur in vaginam solam redacto; petal pallide caerulea, inferius imminutum; staminodia minima et obscuris lobis; capsula elongata tribus cellis infirma cella uno semina et indehiscens, ceterae cellae binis seminibus sed saepe non maturantur; semina magna elongata (*c.* 4 × 1·5 mm.) aspere rugosa et fusca.

Habitat. Loca silvestria.

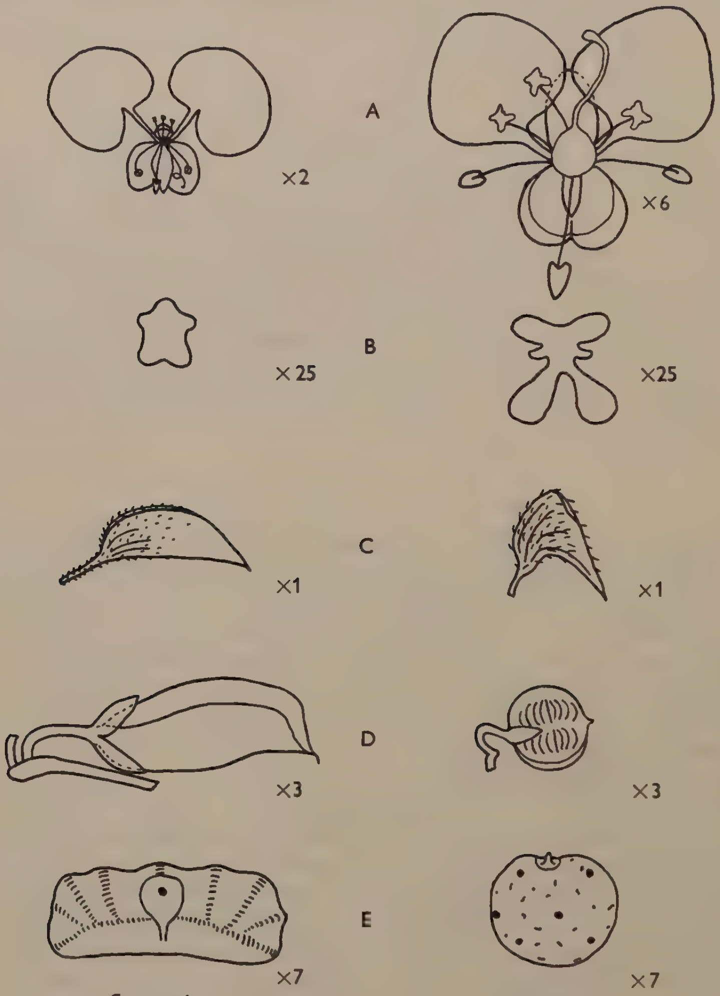
Typus. Morton GC 8061 (B.M., G.C.) ex Ora Aurea.

A very distinct perennial *herb* characterized by its scandent habit, pubescence of colourless ascending hairs with a hooked tip, and the occurrence of the spathes on short branches bearing reduced scale-like leaves. *Stem* bearing very long adventitious roots in its older parts, internodes elongate hairy when young but becoming glabrous. *Leaf* sheath elongate *c.* 20 mm., pubescent; lamina lanceolate *c.* 75 × 22 mm., glabrous apart from the main veins, shortly petiolate. *Spathes* borne on short bracteate inflorescences on peduncles which are as long as the spathes, small (up to 22 × 9 mm.) crescent shaped, not acuminate, margins free or nearly so, containing some mucilage. *Flowers* medium sized *c.* 14 mm., first ones usually male and longly pedicellate, later ones hermaphrodite and very shortly pedicellate. *Petals* pale bluish-violet, the upper pair with a claw of medium length, the basal one ovate-triangular inconspicuous and not exceeding the sepals. *Anthers* 3 yellow with pale yellow filaments; infertile anthers of the staminodes 3 very small and obscurely lobed. *Capsule* elongate apiculate 3-locular, the upper loculi dehiscent 2-ovulate but one or both ovules may frequently be abortive, basal loculus single seeded and indehiscent. *Seeds* large and elongate *c.* 4 × 1·5 mm., brown and coarsely wrinkled, $2n = 28$. An uncommon plant in both secondary and open primary forest.

Exsicc. Morton GC 8061 (B.M., G.C.). Type: Nsawam; GC 8426 (C.G.), dry forest by the Anyaboni to Jaketi road; GC 8424 (G.C.), Mampong Scarp (Akwapim); GC 8241 (G.C.), secondary forest near Bisa; and A551 (B.M., G.C.), Mankrong on the River Affram.

C. aspera Benth. in Hook. *Nig. Fl.* 542 (1849)

A small erect annual *herb* either branched or unbranched and rooting only at the base. Internodes usually long and slender with a band of colourless hairs on alternate sides. *Leaf* sheath loose and membranous, pubescent with short or long colourless hairs; lamina sessile, linear 40 to 100 × 4 to 8 mm., tapered to an acute point and only slightly narrowed to the base, glabrous or pubescent. *Spathes* borne in terminal clusters, shortly stalked, very obliquely triangular with a reflexed base, *c.* 7 × 10 mm., sharply acuminate, prominently veined, glabrous or with colourless bristles, margin fused, mucilage present. *Flowers* very small *c.* 6 mm. diam., hermaphrodite and borne on short pedicels which are included in the spathe. *Petals* white or pale flesh-coloured, the upper pair with a short claw, the lower one very small and ovate-lanceolate. *Anthers* 3 yellow, the middle one larger; infertile anthers of the staminodes 3, the upper and lower lobes well developed,



C. ascendens

Fig. 13.

C. aspera

Fig. 14.

Figs. 13, 14. For explanation see legend for Figs. 11, 12.

spreading and cream coloured, the middle lobes very small spreading and yellow. *Capsule* small globose shortly apiculate and 3-locular, each loculus dehiscent and single seeded. *Seeds* globose with a small apicule, pale brown with darker spots, $2n=28$.

Habitat. Usually growing amongst tall savannah grasses, sometimes on cultivated land, not common.

Exsicc. Morton GC 5292 (B.M., G.C.), GC 25286 (G.C.), GC 25212 (G.C.) and GC 25333 (G.C.), all from Banda, Wenchi area; Morton A104 (B.M., G.C.), GC 25052 (G.C.) and GC 9970 (G.C.), all from Damongo, Northern Territories.

C. **benghalensis** Linn. *Sp. Pl.* ed. i, p. 40 (1743); ed. ii, p. 60 (1762).

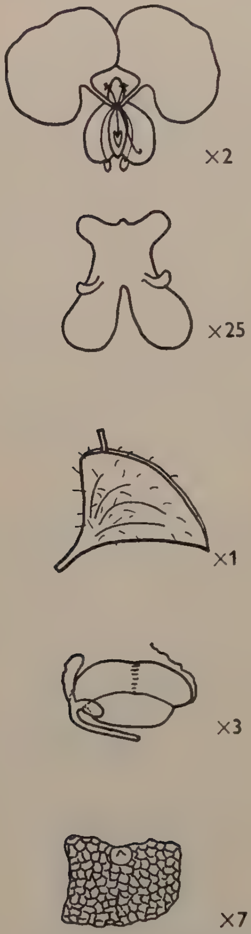
A large straggling *herb* rooting at the nodes and covered in all its parts with a colourless pubescence. *Leaf* sheath loose and pubescent; lamina petiolate, ovate-lanceolate, less than 3 times as long as broad, pubescent. *Spathes* borne several together in the axils of the upper leaves, ovate-triangular, *c.* 15 × 10 mm., margin fused, pubescent and containing mucilage. *Flowers* medium, 10–15 mm. diam.; first flowers frequently male and borne on rather long pedicels, later ones hermaphrodite and borne on shorter pedicels. *Petals* pale violet, sometimes bluish-violet, the upper pair with a short claw, the basal one reduced, subulate and colourless. *Anthers* 3, the 2 lateral ones violet with long violet filaments, the middle one yellow with a shorter violet-coloured filament; infertile anthers of the staminodes 2 small pale yellow, the upper lobes medium sized and spreading, the middle lobes very small and the basal lobes large saccate and slightly divergent. *Capsule* elongate with 3 dehiscent loculi, the 2 upper loculi each having 2 seeds and the basal loculus a single larger and less wrinkled seed. *Seeds* very dark brown, reticulate. $2n=28$ and 56.

This plant occurs in two forms, one diploid with $2n=28$ and the other tetraploid with $2n=56$. In all the Gold Coast and also Cameroons and Nigerian material which we have seen these two forms have been morphologically distinguishable. Further, we have neither discovered intermediate plants in the field nor have we been able to produce them in the experimental garden. The tetraploid differs from the diploid in its larger size, long stout and more straggling branches, and in having red cilia scattered over the whole surface of the leaf sheath and also on the spathe (in the diploid the cilia are colourless or there may be a few red ones confined to the upper margin of the leaf sheath). The two plants further differ in their ecological preferences. The diploid form is a common weed of cultivated and waste land throughout the Gold Coast and elsewhere. The tetraploid form, on the other hand, is a plant of wet forest areas growing in clearings and by roadsides, etc. It has only been encountered in the Gold Coast at Asuboi and at Vane (British Togoland). It is, however, the dominant form in the Cameroons, both in the forest areas and in disturbed places at higher altitudes, e.g. Migeod 2 (K.) collected at 1000 m. at Buea and Morton K22 (G.C.) collected at 1450 m. at Bamenda.

Exsicc. $2n$ plants: Morton A15 (B.M., G.C.), GC 25347 (B.M., G.C.), GC 7858 (G.C.), GC 9835 (G.C.), GC 7889 (G.C.), and P 1297 (G.C.). $4n$ plants: Morton GC 25348 (B.M G.C.), GC 8001 (G.C.), and A102 (G.C.).

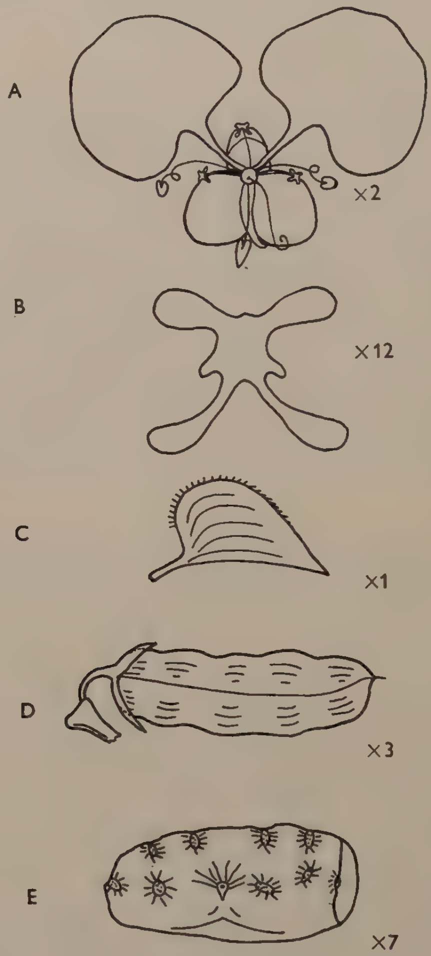
C. **capitata** Benth. in Hook. *Niger Fl.* p. 541 (1849)

A large glabrous, usually erect, branched perennial *herb* not rooting at the nodes. Internodes elongate stout glabrous, rarely puberulous. *Leaf* sheath large, loose, usually glabrous apart from a few dark red cilia on the upper margin, rarely shortly pubescent; lamina shortly petiolate, broadly lanceolate, large *c.* 150 × 40 mm., glabrous and glossy above. *Spathes* terminal, usually several together, almost sessile, *c.* 25 × 13 mm., glabrous or with dark red cilia, margin fused at the base, containing mucilage. *Flowers* large *c.* 20 mm. diam., first flowers usually male and longly pedicellate, others hermaphrodite and shortly pedicellate. Petals golden yellow, the 2 upper with a long claw, the lower one small and subulate. *Anthers* 3 yellow; infertile anthers of the staminodes 3 yellow large, with large spreading upper lobes, small median lobes and spreading spathulate lower lobes. *Capsule* large and very elongate, c. 10 mm. long, slightly apiculate, 2-locular, each loculus dehiscent and 2 seeded. *Seeds* large and elongate with conspicuous deep pits, very pale brown almost white. $2n = 42$.



C. benghalensis (diploid form)

Fig. 15.



C. capitata

Fig. 16.

Figs. 15, 16. For explanation see legend for Figs. 11, 12.

Habitat. Common in primary wet forest.

Exsicc. Adams 2193 (G.C.), 2258 (G.C.), 1943 (G.C.) and 1827 (G.C.); Irvine 1421 (G.C.) and 2616 (G.C.); Johnson 256 (G.C., K.); Morton GC 8095 (B.M., G.C.), GC 8324 (B.M., G.C.), GC 8171 (G.C.), GC 9200 (G.C.), GC 6397 (G.C.), GC 6388 (G.C.) and GC 8444 (G.C.); St Clair Thompson 1520 (G.C.).

C. congesta C.B.Cl. in DC. *Monogr. Phan.* **3**, 160 (1881)

C. condensata C.B.Cl. loc. cit.
C. heudelotii C.B.Cl. loc. cit.
C. amphibia A. Chev. in *Bull. Soc. Bot. France*, **57**, mém. viii. 214 (1911).
C. amphibia var. *hirsuta* A. Chev. loc. cit.
C. congesta var. *hirsuta* Hutch. in *F.W.T.A.* **2**, 320 (1936).

A creeping perennial *herb* rooting at the nodes, glabrous or with long colourless hairs. Internodes glabrous, frequently short and largely covered by the leaf sheaths. *Leaf* sheath large and loose, usually partly or wholly clothed with colourless cilia, rarely glabrous; lamina shortly petiolate, broadly lanceolate *c.* 80 × 25 mm., glabrous or ciliate on the veins. *Spathes* sessile and sunk, either singly or several together, in the axils of the upper leaves, broadly triangular and hardly oblique, *c.* 19 × 16 mm., larger in fruit, margin fused, containing much mucilage. *Flowers* medium, *c.* 15 mm. diam., hermaphrodite and almost enclosed in the spathe. *Petals* very pale violet, almost white, the upper pair with a very short claw, the basal one very small and subulate. *Anthers* 3 yellow, filaments frequently coiled; infertile anthers of the staminodes 2 minute, reduced to a narrow almost unlobed structure. *Capsule* slightly longer than broad with 3 single-seeded loculi, the basal loculus indehiscent. *Seeds* elliptic smooth, dark brown with paler markings. $2n=28$ in both hairy and glabrous forms.

Habit. Common in wet places in the forest areas, rarely on cultivated land.

Exsicc. The glabrous form: Morton P1340 (G.C.), P1318 (G.C.), GC 7947 (B.M., G.C.), GC 7941 (G.C.), GC 8211 (G.C.) and GC 8198 (G.C.). The hairy form: Adams 2004 (G.C.); Morton GC 8057 (G.C.), GC 7884 (B.M., G.C.), GC 7998 (G.C.), GC 8494 (G.C.), GC 8378 (G.C.), GC 8204 (G.C.), GC 8579 (G.C.), GC 7992 (G.C.) and GC 8337 (G.C.). Intermediate plants: Adams 1814 (G.C.); Morton GC 6389 (G.C.).

Note. In most of the strains of this species grown under cultivation the degree of hairiness has decreased with increased shade and water supply and vice versa, but in a completely glabrous strain no effect was obtained from changes in the environment.

C. diffusa Burman f. in *Fl. Ind.* **18**, t. 7, f. 2 (1768)

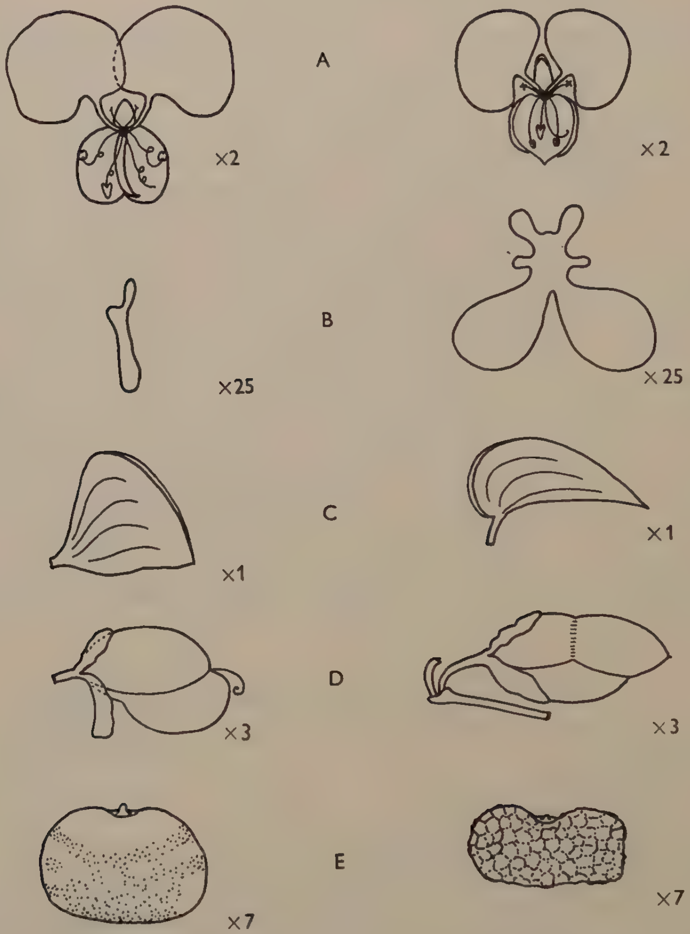
C. nudiflora Linn. *Sp. Pl.* ed. 1 (1753), pro parte, nomen ambig., vide Merrill in *J. Arn. Arb.* **18**, 64–6 (1937).
C. nudiflora in Thiselton-Dyer, *Fl. Trop. Afr.* **8**, i, 36 (1901) et in Hutchinson and Dalziel, *F.W.T.A.* **2**, 318 (1936).

A variable straggling annual or perennial *herb* with glabrous arching internodes, rooting at the nodes. *Leaf* sheaf loose and frequently mottled with dark red markings; lamina usually small *c.* 40 × 16 mm., broadly lanceolate or ovate-lanceolate, rarely larger 80 × 20 mm. and lanceolate, sometimes pubescent in the larger form. *Spathes* borne singly in the axils of the leaves on spreading or reflexed peduncles exceeding half the length of the spathe, small *c.* 17 × 7 mm. in flower, larger in fruit, elongate acuminate with free margins and no mucilage. *Flowers* small *c.* 11 mm. diam., first flowers usually male and borne on long pedicels, others hermaphrodite and shortly pedicellate. *Petals* pale violet, the 2 upper with a short claw, the lower one almost as large sessile and cordate. *Anthers* 3 outer ones black and middle one yellow, with yellow filaments; infertile anthers on the staminodes 2 yellow, the upper and middle lobes small and the basal ones large and saccate. *Capsule* elongate apiculate 3-locular, upper loculi dehiscent and 2-seeded, basal loculus single-seeded and indehiscent. *Seeds* elongate reticulate, dark greyish brown. $2n=28$ in both broad and narrow leaved forms.

Habitat. A weedy plant common in open damp places throughout the Gold Coast. The larger plants with lanceolate leaves appear to be confined to areas north of the forest belt. The normal small plant occurs throughout the country.

Exsicc. Morton P 1435 (B.M., G.C.), A 48 (G.C.), GC 7445 (G.C.), GC 8294 (G.C.), GC 8496 (G.C.), GC 8315 (G.C.), GC 8260 (B.M., G.C.) and GC 9015 (B.M., G.C.)—the small form; Morton GC 8832 (B.M., G.C.) and P 1434 (B.M., G.C.)—the large form.

Note. *Commelina diffusa* is a very widely distributed and variable plant which will probably require subdivision after further study. The two forms mentioned here have remained constant under cultivation, but they appear to be connected by intermediates.



C. congesta

Fig. 17.

C. diffusa

Fig. 18.

Figs. 17, 18. For explanation see legend for Figs. 11, 12.

C. forskalaei Vahl, *Enum.* **2**, 172 (1806)

A small creeping annual *herb* rooting at the nodes. Indumentum variable, glabrous or shortly or longly pubescent with colourless hairs. Internodes elongate, arching, frequently shortly pubescent. *Leaf* sheath short with dark red markings, glabrous or shortly pubescent and with a few long colourless cilia on the upper margin; lamina small *c.* 37 × 13 mm. ovate or elliptic, broadly acute to obtuse, not acuminate, sessile, frequently roughly pubescent with short and long colourless hairs, margin thick and undulate. *Spathes* borne singly on short peduncles in the axils of the upper and mid-stem leaves, small *c.* 12 × 9 mm. obliquely ovate-rotund, obtuse or almost so and very shortly acuminate, margin fused, glabrous or pubescent sometimes with long colourless cilia, mucilage present. *Flowers* small *c.* 12 mm. diam., first flowers male and borne on rather long pedicels, others hermaphrodite and borne on short pedicels. *Petals* a rich pure blue, the upper pair with a short claw, the lower one small and narrowly elliptic. *Anthers* 3 large, blue with yellow pollen, the lateral ones with very stout blue filaments; infertile anthers of the staminodes 3 yellow, the upper and lower lobes large and almost equal, the median ones small. *Capsule* large, longer than broad, not apiculate, 3-locular, the upper loculi dehiscent and 2-ovulate but usually one or both of these are abortive, lower loculus large indehiscent and single seeded. *Seeds* from dehiscent loculi small elongate, smooth and pale brown. Subterranean (?cleistogamous) fruits are produced. $2n=28$.

Habitat. A weed of open waste and cultivated land. Rare in the Gold Coast despite a remark with a plant collected by Saunders that it is 'a common weed in the Northern Territories'.

Exsicc. Morton A 889 (B.M., G.C.), Saunders 3 (K).

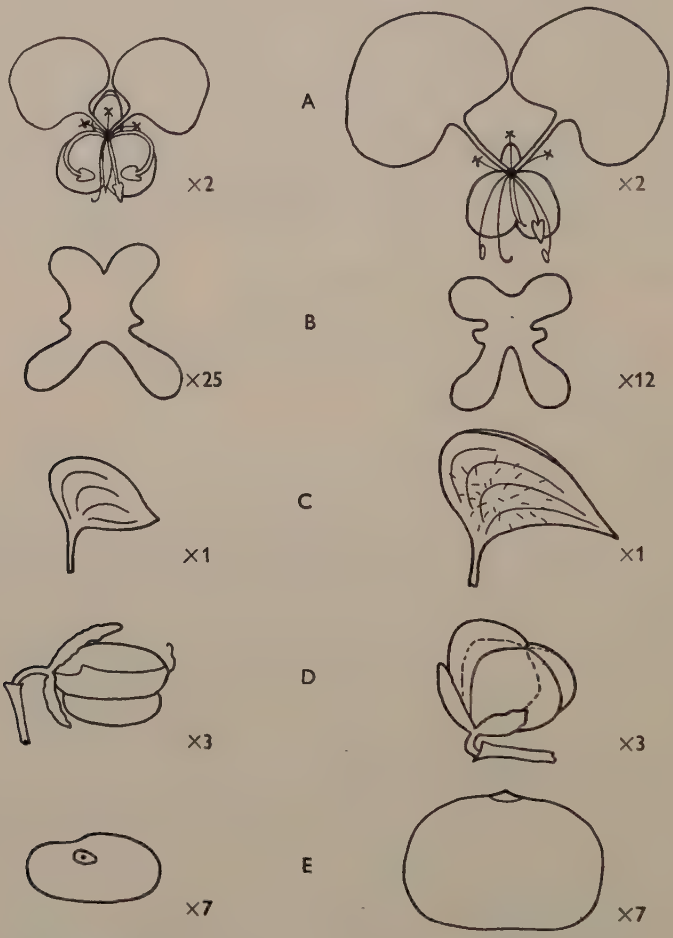
C. gerrardi C.B.Cl. in DC. *Monogr. Phan.* **3**, 183 (1881)

C. aethiopica C.B.Cl. loc. cit. p. 189.
C. vogelii C.B.Cl. loc cit. p. 189.
C. sphaerosperma C.B.Cl. in Thiselton-Dyer, *Fl. Trop. Afr.* **8**, i, 58 (1901).
C. guineensis Hua in *Bull. Mus. Paris*, **1**, 118 (1895).

A medium-sized perennial *herb* varying in its pubescence, habit, leaf characters and spathe arrangement, but recognizable by its spathe, flower, capsule and seed characters. *Stem* usually straggling and frequently somewhat swollen at the base. Internodes usually glabrous, sometimes pubescent with colourless hairs. *Leaf* sheath from 15 to 20 mm. long, usually pubescent with colourless hairs, sometimes glabrous, upper margin with small auricles, ciliate; lamina shortly petiolate, lanceolate, normally *c.* 100 × 20 mm. but broader in ssp. *maritima*, narrower when growing in dry exposed places, glabrous pubescent or setose. *Spathes* borne singly or several together on very short peduncles in the axils of the upper leaves, obliquely ovate-triangular, *c.* 20 × 12 mm., acuminate, margin fused, pubescent or glabrous, containing mucilage. *Flowers* large 20 mm. or more, hermaphrodite and shortly pedicellate. *Petals* bluish-violet, the upper pair with a long claw, the lower one reduced and subulate. *Anthers* dark violet with yellow pollen, lateral ones on long filaments; infertile anthers of the staminodes 3 large (1·3 mm.) yellow, upper lobes large and saccate, median lobes small, basal lobes large spathulate and spreading; filaments all pale violet. *Capsule* globose, not apiculate, with 3 single-seeded dehiscent loculi, frequently one or more loculi abortive. *Seeds* globose, slightly broader than long, *c.* 3·3 × 2·5 mm., with a small apicule at the top, smooth, dark brown sometimes with darker markings.

Though *C. gerrardi* C.B.Cl. is the prior name in the above synonomy it may prove to be short lived. Several allied plants growing in other regions and at present regarded as separate species are probably conspecific with *C. gerrardi*, hence this name may be superseded by an earlier synonym. However, in the light of available information and material the writer is unwilling to extend the above synonomy.

This species is widely distributed in Africa and probably elsewhere in the warmer parts of the world. Its extensive variation makes separation from allied species difficult. Most of this variation is the result of environmental influences, but a certain amount is unaffected by the environment. Amongst the former are leaf characters such as width, texture, glaucous appearance, pubescence and scabrid nature, also the grouping of the spathes and the development of a swollen base to the stem. Minor, genetically controlled variation includes the very rare occurrence of white-flowered plants, also plants with a long slightly deflexed pubescence and others with a stiffly erect habit. The only variation worthy of recognition by a name is a maritime ecotype described below. This plant cannot be equated with any of the plants covered by the above synonomy, and, in view of its ecological importance and distinct appearance in the field, a name is proposed to distinguish it.



C. forskaliae

Fig. 19.

C. gerrardi ssp. gerrardi

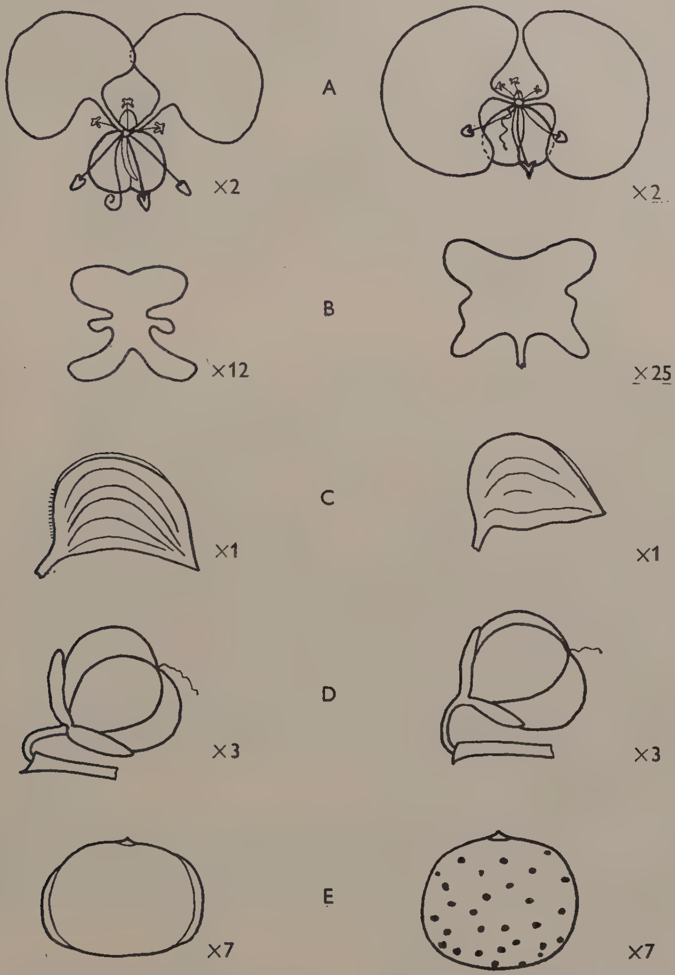
Fig. 20.

Figs. 19, 20. For explanation see legend for Figs. 11, 12.

Subspecies *gerrardi*. A straggling or erect herb, usually pubescent in some of its parts. Leaves lanceolate exceeding 4 times as long as broad, not thick and fleshy, shortly petiolate with very small auricles on the leaf sheath; petiole and upper margin of the leaf sheath with long cilia. Spathe ovate-triangular acute and acuminate, usually pubescent. Flowers large bright blue with a slight violet tinge. Infertile anthers of the staminodes having the upper lobes rounded and with a deep notch between them. Seeds without lateral swollen ridges. $2n = 56$ in all of the many forms examined.

Habitat. Roadsides, secondary forest areas, coastal plains, waste and cultivated land and forest paths. Very common, especially in the southern part of the country.

Exsicc. Morton GC 8338 (B.M., G.C.), GC 8005 (B.M., G.C.), GC 7957 (B.M., G.C.), GC 7994 (B.M., G.C.), P 1392 (B.M., G.C.), A 217 (B.M., G.C.), A 257 (B.M., G.C.) and A 757 (B.M., G.C.). Many other collections, too numerous to cite, are housed in the Gold Coast Herbarium.



C. gerrardi ssp. maritima

Fig. 21.

C. lagosensis

Fig. 22.

Figs. 21, 22. For explanation see legend for Figs. 11, 12.

Subspecies *maritima* J. K. Morton ssp.nov. Ab ssp. quae typus est differt hunc in modum:—planta reptans glabra crassa, folia latiora sessilia in vagina auriculata, spatha ovata obtusa glabra, breviter acuminata, flores pallide-purpurei; semina appendicibus binis angustis lateribus crassis alis similibus instructa.

Habitat. Litus arenosum sub *Cocos nucifera.*

Typus. Morton A 329 (B.M., G.C.) ex Princestown, Ora Aurea.

This plant differs from the type subspecies as follows: a procumbent herb fleshy in all its parts and entirely glabrous apart from a few cilia on the margin of the leaf-sheath auricles, leaves broadly lanceolate, less than three times as long as broad, sessile and distinctly auricled on the leaf sheath, spathe ovate obtuse very shortly acuminate, glabrous apart from a line of very short hairs on the fused margin, flowers smaller and pale violet, infertile anthers of the staminodes less rounded on top and with a shallow notch between the upper lobes, seeds with two narrow thick lateral ridges. $2n=56$.

Exsicc. Morton A 329 (B.M., G.C.), GC 8452 (G.C.), GC 8458 (B.M., G.C.) and P 1388 (G.C.). In addition Morton A 828 (B.M., G.C.) and A 171 (B.M., G.C.) are hybrid plants.

Subspecies *maritima* is a native of the coastal sandbar vegetation under coconut palms. In the west of the country the presence of dense forest and thicket, together with lagoons, behind the sandbar prevents introgression with ssp. *gerrardi* except in the few places where roads have penetrated to the sandbar. In the east, however, the coastal grasslands, in which ssp. *gerrardi* abounds, adjoin the sandbar and introgression has occured, frequently to such an extent that ssp. *maritima* has been completely swamped. There is little doubt that much of this introgression is of recent occurrence, due to the rapid expansion of the coastal grasslands in recent times. This has brought the two subspecies into close contact over a much greater area than would originally exist.

C. lagosensis C.B.Cl. in Thiselton-Dyer, *Fl. Trop. Afr.* 8, 57 (1901).

A creeping softly hairy, rarely almost glabrous, short-lived perennial *herb* rooting at most of the nodes. Internodes weak elongate glabrous. *Leaf* sheath loose, usually mottled with dark red markings, softly hairy with colourless hairs; lamina ovate-lanceolate *c.* 45 × 18 mm. acute, shortly petiolate. *Spathes* usually borne singly on short peduncles in the axils of the upper leaves, small broad *c.* 16 × 11 mm. obtuse shortly acuminate. *Flowers* medium sized, all hermaphrodite and almost enclosed in the spathe. *Petals* pale bluish-violet, the upper pair with a very short claw, arranged at opposite sides of the flower, the basal one minute and subulate (very rarely larger and ovate-cordate). *Anthers* 3 yellow, filaments violet below; infertile anthers of the staminodes 3 pale yellow, the lateral ones larger, upper lobes large and spreading, median and lower lobes medium sized. *Capsule* globose not apiculate with 3 single-seeded dehiscent loculi. *Seeds* globose with a small apicule, smooth, brown with darker markings. $2n=28$.

Habitat. An abundant weed of roadsides and waste and cultivated land in the forest and coastal regions, less common in the north of the country where it usually grows in damp shady places or amongst rocks.

Exsicc. Morton P 1205 (B.M., G.C.), GC 7981 (B.M., G.C.), GC 7915 (B.M., G.C.), GC 8093 (G.C.), GC 7896 (G.C.), P 1224 (G.C.), P 1242 (G.C.), GC 7946 (G.C.), GC 6369 (G.C.), GC 7837 (G.C.), GC 7789 (G.C.), GC 7838 (G.C.), GC 8022 (G.C.), GC 7879 (G.C.), GC 8559 (G.C.), GC 9045 (G.C.), GC 9736 (G.C.) and A 103 (G.C.).

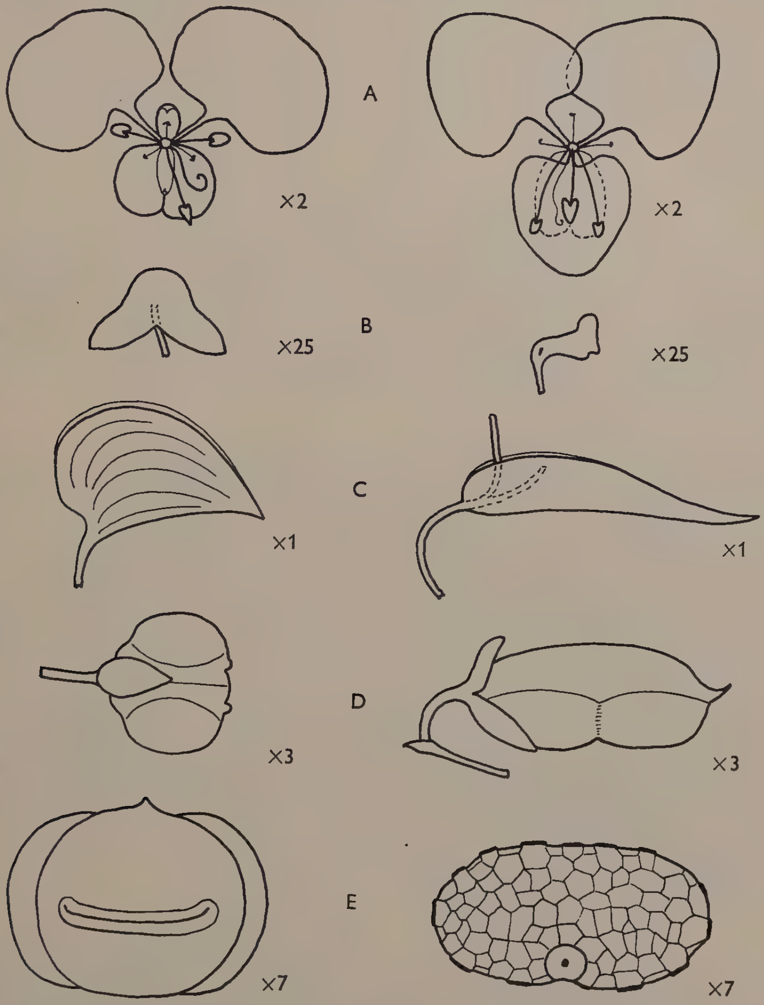
C. livingstoni C.B.Cl. in DC. *Monogr. Phan.* 3, 190 (1881)

A large stout perennial *herb* not rooting at the nodes and usually growing in erect clumps, rarely straggling. Roots thick and woolly. Base of stem swollen, internodes stout elongate glabrous and usually with a reddish coloration. *Leaf* sheath large and loose glabrous or with long colourless hairs; lamina large usually linear-lanceolate *c.* 150 × 14 mm. rarely lanceolate, slightly narrowed into a broad petiole, thick and glabrous with prominent longitudinal veins and a scabrid margin; lower leaves progressively reduced and the lowest ones represented by a brown membranous sheath. *Spathes* borne singly or several together in the axils of the upper leaves on peduncles half their own length, large *c.* 28 × 17 mm. acuminate, margin fused, containing much mucilage, inverting when the capsules mature. *Flowers* large over 20 mm., first ones male and borne on pedicels of medium length, others hermaphrodite and shortly pedicellate. *Petals* bright pure blue, the upper pair with a long claw, the lower one small and subulate. *Anthers* 3; infertile anthers of the staminodes 3 yellow small, shaped like a broad inverted "V". *Capsule* large, as long as broad, with 2 short ridges at the apex, and

2 dehiscent single-seeded loculi. *Seeds* large *c.* 4·5 × 3·5 mm. globose with a broad thickened ridge at each side, smooth and dull, very dark grey, almost black. $2n=56$.

Habitat. Frequent in savannah woodland north of the forest belt.

Exsicc. Morton GC 8434 (B.M., G.C.), A 668 (B.M., G.C.), GC 8553 (G.C.), GC 7322 (G.C.), GC 8785 (G.C.) and GC 8654 (G.C.). Note also Morton A 685 (B.M., G.C.) which is a hybrid with *C. gerrardi.*



C. livingstoni
Fig. 23.

C. macrospatha
Fig. 24.

Figs. 23, 24. For explanation see legend for Figs. 11, 12.

C. macrospatha Gilg & Lederm. ex Mildbr. in *Notizbl. Bot. Gart. Berl.* **9**, 253 (1925)

A glabrous perennial *herb* with slender erect non-rooting branches arising from an elongate branched rhizome. *Leaf* sheath long and narrow, 20–30 mm. long, glabrous apart from a few cilia on the upper margin; lamina linear-lanceolate *c.* 90 × 11 mm. glabrous with a scabrid margin; lower leaves reduced to a brown membranous sheath. *Spathes* borne singly in the axils of the upper leaves on peduncles as long as the spathes, elongate *c.* 30 × 7 mm. in flower and 60 × 9 mm. in fruit, with almost parallel sides gradually acuminate from the middle, margins free, without mucilage. *Flowers* large *c.* 19 mm., first flowers male and borne on very long pedicels, others hermaphrodite and shortly pedicellate. *Petals* bright pure blue, the upper pair with a long claw, the lower one as large as the others but almost sessile. *Anthers* 3; infertile anthers of the staminodes 3 minute, not lobed, white. *Capsule* large elongate apiculate, 3-locular when young but 2-locular at maturity, fertile loculi 2 seeded and dehiscent. *Seeds* large elongate reticulate covered with a white powder. $2n=28$.

Habitat. Cultivated savannah. In the Gold Coast only collected near Ejura and on the edge of the Affram Plains near Mankrong.

Exsicc. Morton GC 9842 (B.M., G.C.), A 721 (B.M., G.C.), GC 9748 (G.C.), and GC 9730 (G.C.).

C. macrosperma J. K. Morton sp.nov.

Herba patula perennis subglabra hunc in modum distincta;—folia elliptico-lanceolata, spathae aut singillatim aut aliquot in uno loco enascentes e brevibus inflorescentiis in axillis superiorum foliorum tenues glabrae oblique ovatae breviter ac late acuminatae margine iuncto, flos parvus albus, capsula magna 7 mm. longus emarginatus duabas cellis cellae singulis seminibus, semina magna 4·5 × 2·5 mm. reticulata latis pallido-aureo-fuscis lineis et nigro-fuscis cavis.

Habitat. In silvas umidas.

Typus. Morton A 109 (B.M., G.C.) ex Kibbi, Ora Aurea.

A spreading perennial *herb* with stiff slender stems, not rooting at the nodes. *Leaf* sheath slender shortly pubescent; lamina elliptic-lanceolate broad *c.* 65 × 27 mm. rounded and shortly petiolate at the base, acutely acuminate at the apex, thin with prominent transverse veins, very thinly pubescent on both surfaces. *Spathes* borne singly or several together on short bracteate inflorescences in the axils of the upper leaves, small *c.* 17 × 11 mm. with prominent transverse veins, obtuse with a very short acumen, containing mucilage. *Flowers* small and very delicate *c.* 11 mm. diam. all hermaphrodite and very shortly pedicellate. *Petals* white, the upper pair with a short claw, the lower one medium sized and ovate. *Anthers* 3; infertile anthers of the staminodes 3 cream, with large rotund upper lobes, medium-sized deflexed basal lobes and small spreading middle lobes; filaments all colourless. *Capsule* large 7 mm. long oblong flattened emarginate with 2 single-seeded dehiscent loculi. *Seeds* very large 4·5 × 2·5 mm. oblong reticulate with broad pale brownish-orange ridges and dark brown hollows. $2n=20$. The plant grows in wet forest areas especially under cocoa.

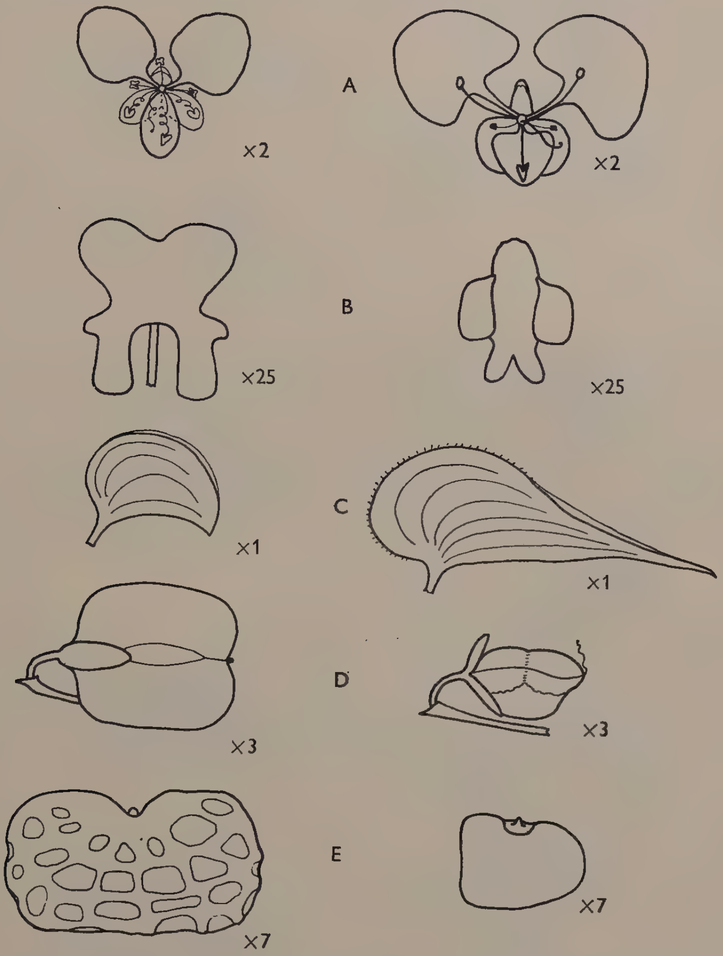
Exsicc. Irvine 533 (G.C., K.), Morton A 109 (B.M., G.C.)

C. thomasii Hutch. in *Kew Bull.* 1936

A large longly straggling subglabrous or softly pubescent perennial *herb* rooting at the nodes. Internodes elongate glabrous, rarely shortly pubescent when young. *Leaf* sheath loose, medium sized 20–30 mm. long, ciliate on the margin and glabrous or with long colourless hairs on the surface; lamina narrowly lanceolate *c.* 80 × 14 mm. rounded at the base, glabrous or softly pubescent, margins scabrid. *Spathes* borne singly in the axils of the leaves on deflexed or arcuate peduncles half as long as the spathes, large from 30 to 70 mm. long, broad at the base and immediately tapered into a large acumen, glabrous or softly hairy with free margins and no mucus. *Flowers* medium sized *c.* 15 mm. shortly pedicellate and usually hermaphrodite. *Petals* very pale violet, almost white, the upper pair with a rather short claw, the lower one medium-sized cordate and without a claw. *Anthers* 3 yellow with white filaments; infertile anthers of the staminodes 2 small, upper lobes absent, median lobes rather large rotund, lower lobes small and connivent, white with yellow median lobes. *Capsule* longer than broad apiculate 3-locular, upper loculi dehiscent and 2 seeded, basal loculus indehiscent and single seeded. *Seeds* rather small elongate brown, smooth when viewed under a low magnification but finely reticulate under a higher magnification. $2n=56$.

Habitat. Common in damp places in secondary forest areas.

Exsicc. Morton GC 8339 (B.M., G.C.), GC 8234 (B.M., G.C.), GC 8053 (B.M., G.C.), GC 7753 (G.C.), GC 7967 (G.C.), GC 7999 (G.C.), GC 7883 (G.C.), GC 8199 (G.C.), GC 8427 (G.C.), GC 8235 (G.C.), GC 8205 (G.C.), GC 7937 (G.C.), GC 8068 (G.C.), GC 8028 (G.C.), GC 7803 (G.C.), GC 6390 (G.C.), GC 8003 (G.C.), GC 7859 (G.C.), GC 6413 (G.C.), GC 8363 (G.C.), GC 8326 (G.C.) and GC 8332 (G.C.).



C. macrosperma

Fig. 25.

C. thomasii

Fig. 26.

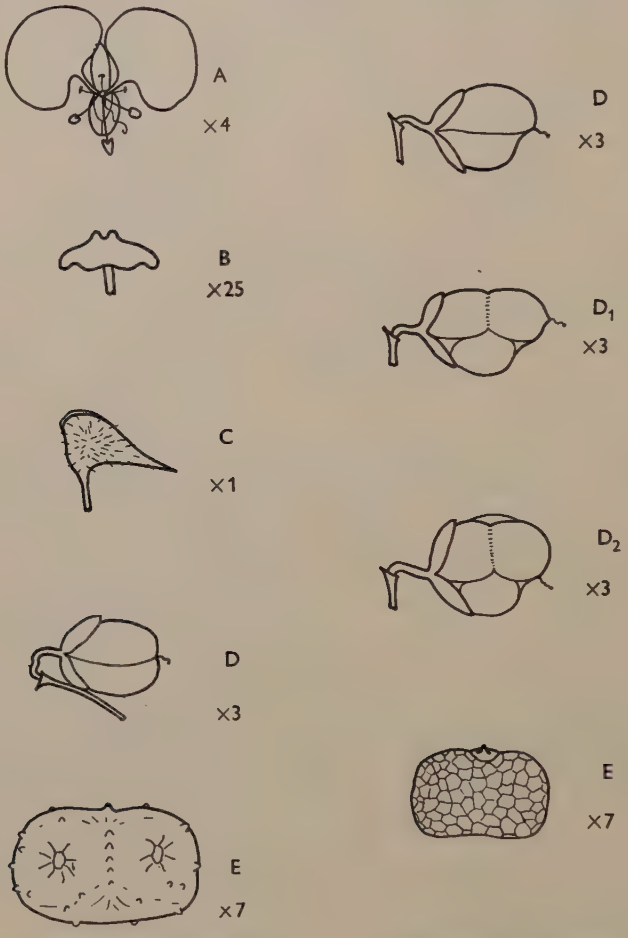
Figs. 25, 26. For explanation see legend for Figs. 11, 12.

C. umbellata Thonn. in Schumach. *Beskr. Guin. Pl.* p. 21 (1827).

Inc. *C. gambiae* C.B.Cl. in DC. *Monogr. Phan.* **3**, 146 (1881).

A small usually straggling annual *herb* rooting at the nodes. Internodes elongate glabrous apart from an alternate band of hairs. *Leaf* sheath short, loose, usually with prominent dark red veins, glabrous or with long colourless hairs; lamina linear up to

100 mm. long and 5 mm. broad, rather thick, usually glabrous sometimes with long colourless hairs. *Spathes* borne singly on short peduncles in the axils of the mid and upper leaves, small 13 × 5 mm. recurved sharply acuminate, usually with long colourless cilia concentrated in the middle of each side rarely glabrous, margin fused, mucilage present. *Flowers* small *c.* 6 mm. diam. shortly pedicellate and mostly hermaphrodite. *Petals* pale orange-brown (the buds and faded flowers appear bluish in colour), the upper pair very broad and with a short claw, the lower one minute and subulate. *Anthers* 3 black with yellow pollen; infertile anthers of the staminodes 3 very small much broader than long and obscurely lobed, pale yellow; all filaments dark red. Style dark red with a yellow tip.



C. umbellata var. *umbellata*

Fig. 27.

C. umbellata var. *gambiae*

Fig. 28.

Figs. 27, 28. For explanation see legend for 11, 12.

Var. *umbellata*. Capsule large slightly broader than long not apiculate with 3 single seeded dehiscent loculi, frequently one or more of the loculi abortive. Seeds large *c.* 3·3 mm. long oval somewhat flattened with 2 black pits with radiating ridges on the upper surface, also usually having some scattered light-coloured tubercles, ground colour pale brown. $2n = 28$.

Habitat. Not uncommon in cultivated savannah country.

Exsicc. Adams 1855 (G.C.); Morton A 105 (B.M., G.C.), GC 6212 (G.C.), A 106 (G.C.), GC 9731 (G.C.), GC 9852 (G.C.) and GC 9967 (B.M., G.C.).

Var. *gambiae* (C.B.Cl.) J. K. Morton. Capsule with 3 dehiscent loculi one or more of which may be abortive, loculi 2 ovulate when young but usually only one or two of the loculi are 2 seeded when mature. The capsule shape depends on the number and position of the seeds which develop (see Fig. 28 D, D_1, and D_2). Seeds small and almost globose *c.* 2·3 mm. diam. dark brown with pale reticulate ridges. $2n=28$.

Habitat. In marshy uncultivated savannah, rarely in damp cultivated savannah. Less common than the type variety.

Exsicc. Morton GC 9829 (B.M., G.C.), GC 9905 (B.M., G.C.), GC 9973 (B.M., G.C.), GC 9482 (G.C.) and GC 9969 (G.C.).

C. gambiae C.B.Cl. and *C. umbellata* Thonn. are clearly minor variations of the same species. They appear to differ only in their seed and capsule characters, though the former is frequently a small erect almost unbranched plant while the latter is rather stout and much branched. On occasions they are to be found growing together and then intermediate plants frequently occur, e.g. at Tamale (Morton GC 9922, B.M., G.C.) and Banda, Wenchi district (Morton GC 25290, G.C.).

ACKNOWLEDGEMENTS

The writer is indebted to Mr E. R. Vaughan, Curator of the Botanic Gardens in the University College of the Gold Coast, for his assistance and co-operation in the cultivation of the material used in this research; also to the Director of the Royal Botanic Gardens at Kew and to the Keeper of the Department of Botany in the British Museum for permission to examine the herbarium material in these institutions. He is also grateful to Mr J. P. M. Brenan for advice and assistance during the course of this work, and to Mr R. H. Howorth for assistance in the preparation of the Latin diagnoses.

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Cytotaxonomy of Spirogyra I, S. submargaritata, S. subechinata and S. britannica. By M. B. E. Godward, Queen Mary College, London.

(With Plates 51–53 and 8 Text-figures)

[Read 19 January 1956]

INTRODUCTION

It is proposed to publish a series of papers, of which this is the first, on the cytotaxonomy of *Spirogyra*; and it is hoped at least to deal with all the British species, which constitute about 20 % of those described. The genus contains a formidable number of species and many have been reported only once, from a single locality. It would not be surprising to find rarely reported species in Britain; and indeed I have recently collected *S. oblata* Jao, previously recorded only from Hangchow, China, from two British localities. It has been found necessary to describe three new species. An account of these forms the main part of the present paper.

To the late Prof. F. E. Fritsch, F.R.S., I am indebted for generous help in coping with the identification of species and with taxonomic problems which have arisen from time to time; to Dr George Taylor, Keeper of Botany, British Museum (Natural History) for discussion of taxonomic problems and partial editing of the manuscript; to Mr R. Ross, British Museum (Natural History), for advice and encouragement and for the Latin diagnoses; and to the Keepers of the herbaria at the British Museum, the Royal Botanic Gardens, Kew, and the Riksmuseet, Stockholm, for access to specimens in their charge.

Examination of a number of species of *Spirogyra* has led me to the conclusion that cytological characters, as shown in the resting nucleus and at mitosis, can be used for taxonomic purposes in conjunction with morphological characters, which hitherto have alone been used in the classification of the genus. Of these morphological characters, those of the zygospore, on which species identification ultimately rests in the existing systems of classification, alone seem to be critical. Too often the experimenter, whether physiologist or cytologist, or the field worker, whether taxonomist or ecologist, cannot obtain these zygospores. As an example, a pond has been under continuous observation for sixteen months. During that time it has contained a species of *Spirogyra* in full vegetative development, but there is no sign as yet of conjugation. Consequently, the identification of the species is impossible from any work of reference now in existence. A tentative identification has been made on the basis of the cytological characters.

Prof. F. E. Fritsch advised me that the late G. S. West thought that the characters of the chloroplasts and pyrenoids might prove taxonomically useful and consequently camera lucida drawings of structures in vigorous vegetative filaments were made. My observations suggest that the chloroplast is of very variable appearance in a single species. Its morphological characters seem to depend to some extent on the conditions under which the filament is growing, particularly the intensity of the light. The state of the filament, whether vegetative, approaching conjugation, conjugating, or post-conjugative, may also have a profound effect on the appearance of the chloroplast, even in those cells which are not taking part in the conjugation process. Even where a chloroplast character is extreme, as for example where there is a complete lack of spiralization, it tends to be shown by more than one species. It may be doubted whether chloroplast characters will be used for taxonomic purposes in the future more extensively than they are to-day.

On the other hand, the cytological characters in this genus appear to be as fixed and definite as in the higher plants. No two species have yet been found, moreover, to resemble one another in all aspects of their nuclear cytology. Thus these may under favourable circumstances offer a means of identification of the species, in the absence of the zygospore.

The methods of staining which will give results easily have already been described (Godward, 1950*a*), and it may be emphasized that all species show characters of importance in the resting nucleus. It must be admitted that some species are easier to investigate cytologically than others, and the following difficulties may arise.

(1) Mitosis may be very slow or metaphase very rare under ordinary conditions, and thus to obtain a count may need considerable perseverance.

(2) The mid-prophase stages, showing the nuclear organizing (N.O.) chromosomes most favourably, may be very rare.

(3) A thick mucilage sheath may be an obstacle to fixing fluids and lead to bad fixation.

(4) The nuclear structures may be very fragile, necessitating especial care in preparation.

(5) The cytological structure may be inherently difficult to see under any circumstances. For example, in *S. setiformis* (confirming Geitler and others) the chromosomes are almost unstainable and are embedded in a large mass of intensely staining material.

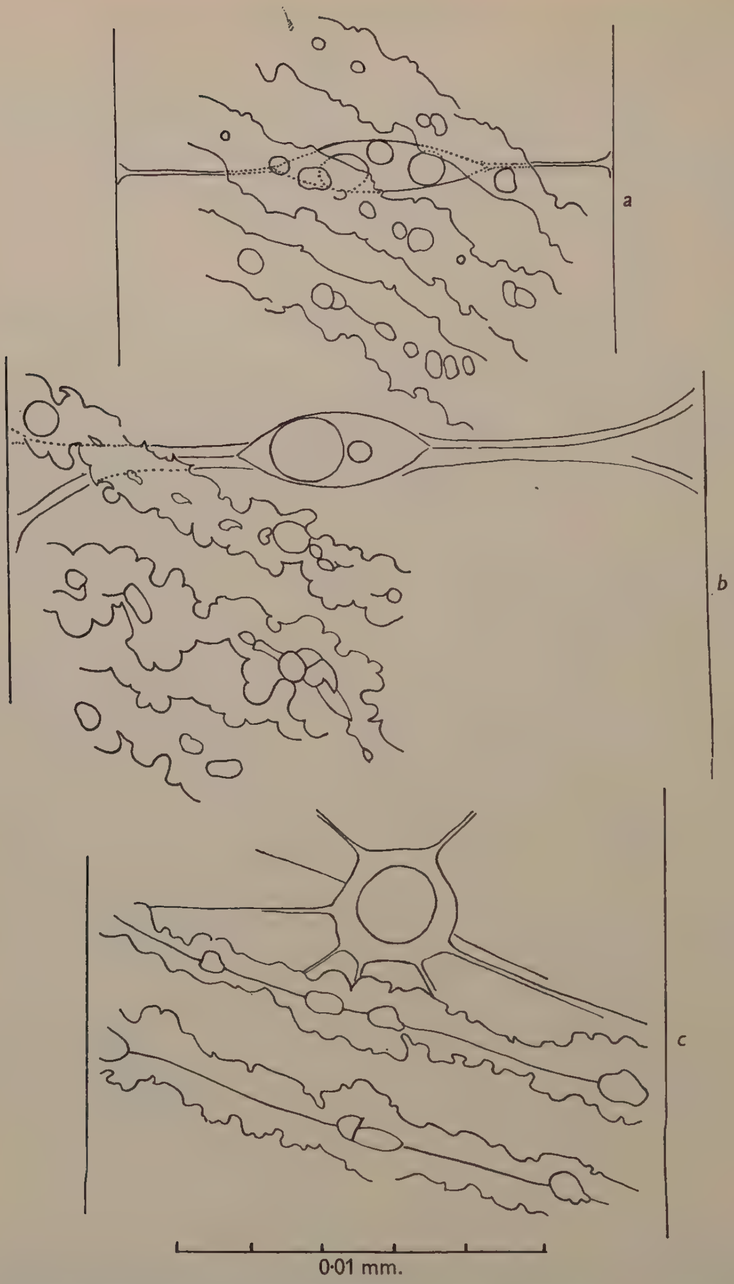
The number of species presenting such difficulties is apparently small, although it may be that in some cases it will prove to be impracticable for the ordinary investigator to use the cytological criteria. In most species at least the characters of the resting nucleus can be used as taxonomic characters, and in some those of the mitotic nucleus are also surprisingly easy to observe.

The cytological characters are most easily appreciated from illustrations and some of the most interesting figures have already been published (Godward, 1950*a*, *b*, 1953, 1954). In these papers a number of special features of *Spirogyra* cytology are described. All the species have characters of importance in the resting nucleus. These are shown in the chromocentres, the nucleolar-organizer tracks in the nucleolus (Godward, 1950*a*) and in the shape of the nucleus. The chromocentres may be large or small, few or numerous, present or absent. The organizer tracks in the nucleolus may be clear or obscure, much or little coiled, surrounded by concentric membranes or not, clearly countable or uncountable, and accompanied by much or little additional nucleolar material (Godward, 1953). The nucleus may be lenticular or spherical in shape and the suspensory cytoplasmic strands distributed differently in each case. Except for the shape of the nucleus, it is unlikely that these characters can be adequately observed without staining, which takes only a few minutes (see Godward, 1950*a*).

At mitosis, there is great variation among the different species in the size, numbers, and characters of the chromosomes, particularly in regard to centromere organization (Godward, 1953, 1954), and also in the numbers and character of the N.O. chromosomes, and the distribution of the nucleolar substance (Godward, 1950*a*, *b*, 1953, 1954). The species are readily recognizable from these cytological characters alone.

DESCRIPTIONS OF NEW SPECIES

A new morphological character will be used in the descriptions, namely the proportion of cells in the filament which form conjugation tubes. Species may be placed in two groups: first, those in which every cell or almost every cell along a considerable length of filament forms a conjugation tube; and secondly, those in which only isolated cells, or small groups of cells, form conjugation tubes. These conjugating cells are separated by intervening stretches of filament in which the cells do not conjugate. This second condition is, or tends to be, associated with a difference in size between the two conjugating cells or gametangia, and with a wide type of conjugating canal. It thus constitutes an approach to the condition found in *Sirogonium*, where only occasional cells conjugate, the conjugation canal is very wide and there is a marked difference in the sizes of the two gametangia.



Text-fig. 1. Camera lucida drawings of chloroplasts and nuclei. Drawings made from living material in vigorous growth. (*a*) *S. submargaritata*. The edges of the chloroplast are not deeply cut; the lens-shaped nucleus, which shows three of the four possible nucleoli, is suspended by almost a single row of protoplasmic strands around the edge of the lens. (*b*) *S. subechinata*. The edges of the chloroplast are deeply cut; the nucleus is lens-shaped but not so flat as in the preceding species. It contains one nucleolus and a sphere of unorganized nucleolar material; it is suspended by marginal strands around the edge of the lens; these strands are more numerous than in the preceding species and there is almost a double row of them. (*c*) *S. britannica*. The chloroplasts have a well-marked midrib; the nucleus is roughly spherical, its suspensory strands being numerous and concentrated into two groups at its 'poles' and not into a single equatorial group as in the other species. (All × 1000.)

Spirogyra submargaritata Godward, n.sp. [in *Ann. Bot.* (N.S.), **17**, 404, 1953; *nom. nud. sine* lat. diag.]

Filament 70–100 μ in breadth; cells 100–192 μ long; chloroplasts 8–10, number of turns of chloroplast 1 or less than 1; septum simple; most cells of filament conjugate. Zygospores 50 × 50 μ to 70 × 70 μ in breadth, 70–75 μ long, mesopore surface smooth, yellow-brown. Dimension of resting nucleus transverse to filament 30–50 μ, longitudinal to filament *ca.* 20 μ; nucleoli 4 or fewer, diameters of nucleoli 3–10 μ; chromocentres prominent. Number of chromosomes 38, including 4 N.O. chromosomes; N.S. forms a plate at metaphase and anaphase; chromosomes 3–0·5 μ long; three types of chromosome are present with respect to the centromere organization—those with a localized median centromere, those apparently polycentric with only 2 or 3 centromeres, and dot-like chromosomes, in which the centromere region cannot be distinguished from any other region.

Filum 70–100 latum, chlorophora 8–10 qua 1 aut minus quam 1 rotatio in cellula quaque faciunt; septum simplex. Zygospori 50 × 50–70 × 70 μ diam., 70–75 μ long., mesospori colorati. Chromosomae 38, nucleoli 4 aut pauciores. *Typus* in Herb. Mus. Brit., coll. Alg. prep. micr. no. 5987 (holo.), 5988, 5989 (syn.).

This species has been collected from three localities in Essex and one in the Lake District.

It is usually rather light green, the chloroplasts being slender and well separated from one another. When there is rapid cell division the chloroplasts are at an angle of about 45 degrees to the septum; when the cells are not dividing so rapidly they are longer and the chloroplast tends to become almost longitudinal in the cells. The disposition of the chloroplast in the actively dividing cell, and the shape of chloroplast and pyrenoids, are shown in the camera lucida drawing (Text-fig. 1*a*). This also shows the shape and disposition of the nucleus.

The zygospores are distinguished by their almost spherical shape and smooth yellow-brown mesospore. Conjugating filaments and mature zygospores in outline are shown in Pl. 51, fig. 1 and Text-fig. 2.

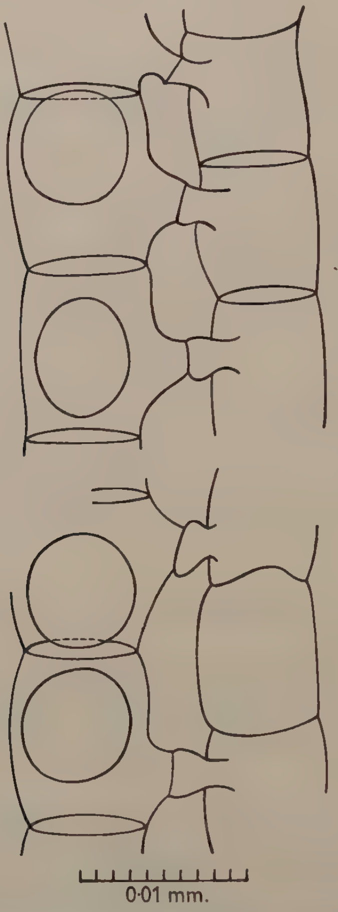
In stained material the chromocentres are found situated near the periphery of the resting nucleus; they are rounded, densely staining and show no internal details; four are attached to the nucleoli. These may or may not be fused together, so that there may be any number of nuclei from one to four; little internal structure can be seen in them (Pl. 52, fig. 1).

The chromosomes, some of which show parallel separation of chromatids while others do not, are described and figured elsewhere (Godward 1953, 1954). Metaphase is shown in Text-fig. 3*b*, where the four longest chromosomes are the N.O. chromosomes. Anaphase, flattened and showing two chromatid plates, is seen in Pl. 52, fig. 2 and Text-fig. 3*a*. Both anaphase and metaphase plates show the chromosomes embedded in nucleolar substance.

Comparison with other species

In the dimensions of the filament and zygospore, there is some approach to the species *S. majuscula* Kutz., *S. orthospira* Naeg., *S. ternata* Ripart and *S. margaritata* Wollny. The epithet *submargaritata* was adopted for the new species at the suggestion of the late Prof. F. E. Fritsch, because both show the nearly spherical shape of the zygospore. It is, however, quite unlikely that there is any close relationship between the two species. Though imperfectly described, the figure of *S. margaritata* Wollny in Hedwigia, 1877, clearly shows that it is characterized by only a proportion of the cells of the filament taking part in conjugation, these being separated by intervening non-conjugant cells. This feature is not found in *S. submargaritata*. Other differences lie in the small size of the zygospore relative to the containing cell and the shape of the resting nucleus, in *S. margaritata*. It has not been possible to obtain herbarium material (exsiccata) of

S. margaritata. Exsiccata of the other species concerned have been examined, all from the Kew Herbarium unless otherwise stated. In *S. majuscula* (exsiccata of Wittrock and Nordstadt, Lagerheim, and Borge from the Riksmuseet, Stockholm) the mesospore was not smooth; in *S. orthospira* (exsicc. Collins Holden and Setchell) the septum was not simple; and in *S. ternata* (exsicc. Teodoresco) the zygospore was ovoid, rather than spherical as in *S. submargaritata.*



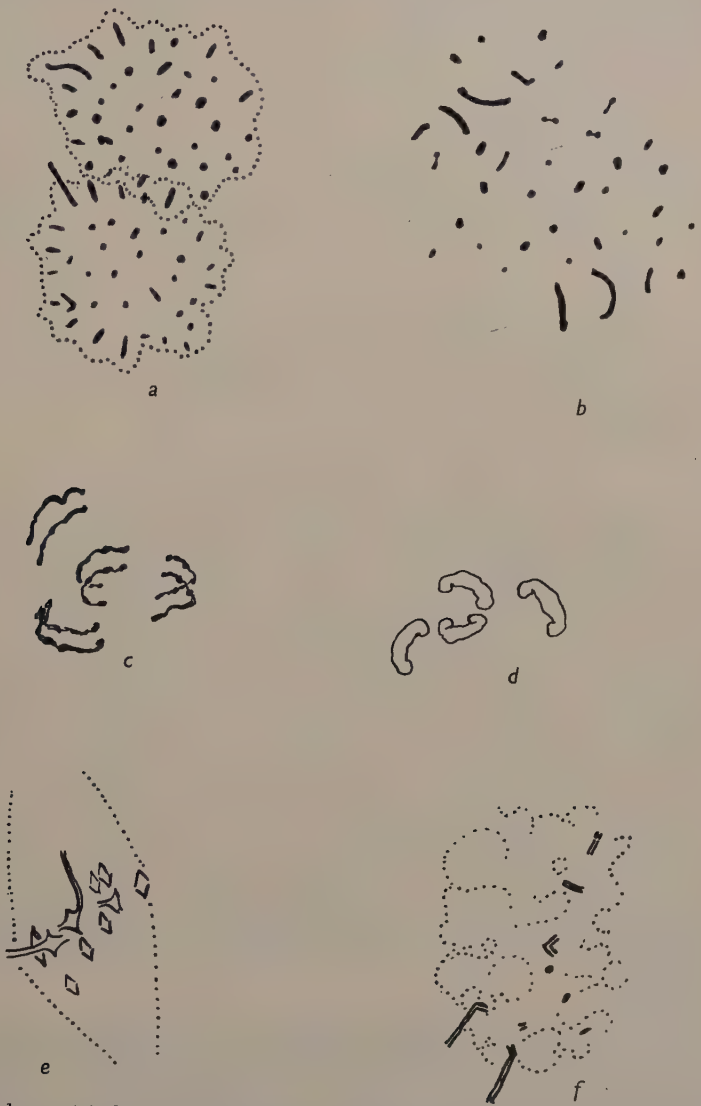
Text-fig. 2. *S. submargaritata*, conjugated filaments and zygospores (× 220).

Spirogyra subechinata Godward, n.sp. [in *Ann. Bot.* (N.S.), **17**, 404, 1953; *nom. nud. sine* lat. diag.]

Filament 80–100 μ in breadth, cells 60–200 μ long: chloroplasts 7–8, number of turns of chloroplasts 1; septum simple; only a proportion of cells of filament conjugate. Zygospores 110 μ in breadth, 140 μ long, mesospore surface subechinate, yellow-brown. Dimension of resting nucleus transverse to filament up to 24 μ, longitudinal to filament to 12 μ; nucleoli usually 1, occasionally 2, diameter of single nucleolus 7–8 μ; chromocentres prominent, thread-like. Number of chromosomes 4, including 2 N.O. chromosomes; N.S. forms a diffuse plate at metaphase; length of chromosomes 4·5–6 μ; chromosomes probably polycentric (they could be described as without localized centromere or with a 'diffuse' centromere).

Filum 80–100 latum; chlorophora 7–8 qua 1 rotatio in cellula quaque faciunt; septum simplex; zygospore 110 μ diam., 140 μ longi; mesospori colorati, subechinati. Non omnes quae in filamento continentur cellae se conjugant. Chromosomae 4 quarum 2 nucleos constituunt. *Typus* in Herb. Mus. Brit., coll. Alg. prep. micr. no. 5993 (holo.), 5994 (syn.).

I have collected this species only once, in southern England. When handled in the field, it has some of the characteristics of *S. crassa*, being light green in colour, delicate and brittle when touched. Many of its other characters enumerated below are also found in *S. crassa* which I regard as a closely related species. The cells tend to be short,



Text-fig. 3. Cytology. (*a*) *S. submargaritata* anaphase plates, the chromatids surrounded by nucleolar substance (× 2000). (*b*) *S. submargaritata*, metaphase, the four long chromosomes are the N.O. chromosomes (× 2000). (*c*) *S. subechinata*, very early anaphase; the chromatids are parallel as they separate, having no localized centromere (× 1500). (*d*) *S. subechinata*, metaphase, four large chromosomes of sinuous shape. (*e*) *S. britannica*, beginning of anaphase; the chromatids are just separating, first at the region which contains the localized centromere. In these 'normal'-looking chromatids the centromere goes first to the pole and the arms of the chromatids lie in line with the spindle (see Godward, 1953, pl. I, fig. 3, and text-fig. 6). (*f*) *S. britannica* prophase, showing 2 long N.O. chromosomes, 3 medium-sized and 5 small ones. Nucleolar substance is lying round them in the form of membranes and streamers (× 3500).

the nucleus lenticular; these features together with the chloroplast are shown in text-fig. 1*b*. Conjugating filaments and zygospores in outline are shown in Text-fig. 4 and Pl. 51, figs. 2, 3. Pl. 51, fig. 3, shows the conjugating filaments before fusion of gametes has occurred; the restriction of conjugation to isolated pairs or small groups of cells will be noted, also the greater size of the female gamete, the altered appearance of the chloroplasts in the gametes—they are shorter and thicker, darker green, contain oil as well as starch—and the wide conjugation canals. In Text-fig. 5 and Pl. 53, figs. 1–2, an attempt is made to show the mesospore surface but this is difficult since this surface has considerable thickness. At the lowest level is an irregular network of thickening material from which numerous small projections in the form of rods or blunt spines grow out. The network is laid down first, and as the zygospore matures the rods develop and lengthen. This structure is of a golden brown colour, and it appears that a transparent colourless substance fills the interstices between the rods. The general appearance is here described as subechinate.

Cytologically the species is easy to investigate. Its metaphase is readily obtained and shows four long chromosomes (Text-fig. 3*d*, and Godward (1953), Pl. XXIII, fig. 1, and (1954), pl. V, figs. 1 and 2) embedded in nucleolar substance which becomes more diffuse the farther it is from the chromosomes. Details of mitosis are described in the two papers quoted above. Anaphase (Text-fig. 3*c*) shows parallel separation of chromatids typical of the polycentric chromosome. The chromocentres show in the resting nucleus (Text-fig. 8*b*) a thread-like form, the threads being irregularly disposed in 'relic coils'; they are well marked and rather large and few. The nucleolus may at times show rather vaguely the organizer tracks as in *S. crassa* (Godward, 1950).

Comparison with other species

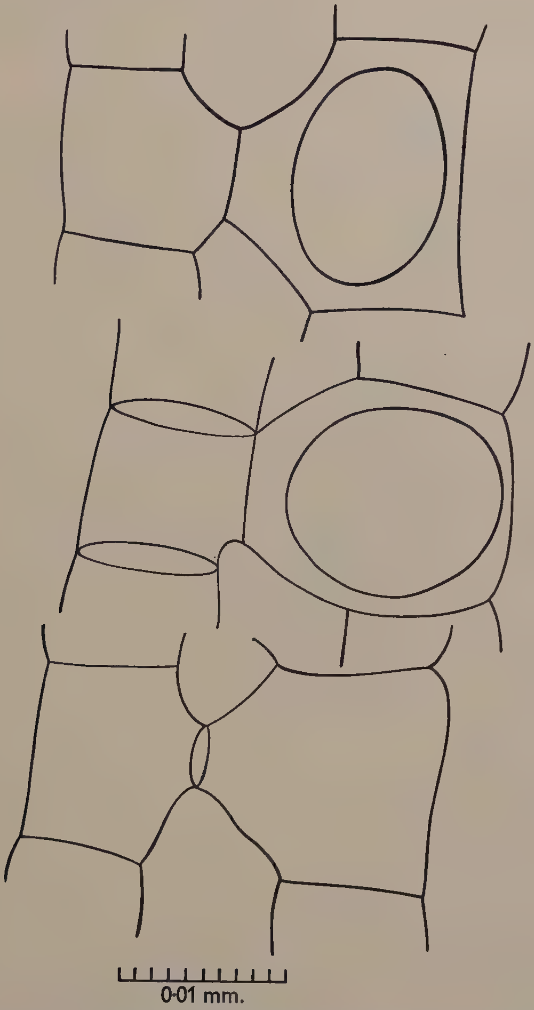
Of the species figured by Kolkwitz and Krieger, only *S. margaritata* and *S. echinata* Tiffany show such wide conjugation canals, together with the spacing-out of the pairs of conjugating cells. It is true that some of their figures include too few cells to show whether this feature is present or not as, for instance, in *S. crassa*. This species is clearly not *S. margaritata* or *S. crassa*, but strongly resembles *S. echinata* Tiffany. It differs, however, in the following characters: the zygospores are bigger, the number of chloroplasts is never as low as four and the rods on the mesospore do not project into the exospore. In view of these differences I have described the plant as *S. subechinata*. It is possible that *S. echinata* and *S. subechinata* are conspecific, since the text and figure of Kolkwitz and Krieger 1941 do not altogether agree as to the projection of the mesospore rods into the exospore, but I have been unable to obtain Tiffany's authentic material for comparison.

Two other species have been described as having four chromosomes. *S. ternata* Ripart, according to Merriman (1916), has 'about 4' chromosomes. *S. longata* (Vauch.) Kutz. was stated to have 4 chromosomes by Chmielewski (1890), but Tröndle (1911) gave the number as 10 to 12. One can hardly doubt that two species have been confused under the name of *S. longata*. Morphologically, neither *S. ternata* nor *S. longata* could be confused with *S. subechinata*.

Spirogyra britannica Godward, n.sp. [in *Ann. Bot.* (N.S.) **17**, 404, 1953; *nom. nud. sine* lat. diag.].

Filament 80–90 μ in breadth, cells 140 to 260 μ long, chloroplasts 3–4, number of turns of chloroplast up to 6; septum simple. Zygospores 70–85 μ in breadth, 100–150 μ long, mesospore smooth, very pale yellow, almost colourless. Dimension of resting nucleus transverse to filament 20–34 μ, longitudinal to filament 14–19 μ; nucleoli 1 sometimes 2, diameter of single nucleolus about 9 μ, chromocentres not visible. Number of chromosomes 10, including 2 N.O. chromosomes; N.S. concentrated around metaphase plate, lengths of chromosomes 0·5–2 μ, chromosomes with localized apparently terminal or subterminal centromeres.

Filum 80–90 μ latum, chlorophora 3–4, qua 6 aut pauciores rotationes in cellula quaque faciunt; septum simplex; zygospori pleni olei fulvi, 70–85 μ diam., 100–150 μ longi; mesospori vix flavi, leves. Chromosomae 10; nucleoli 2 aut saepius 1; chromosomae 2 quae nucleos constituunt. *Typus* in Herb. Mus. Brit., coll. Alg. prep. micr. no. 5990 (holo.), 5991, 5992 (syn.).

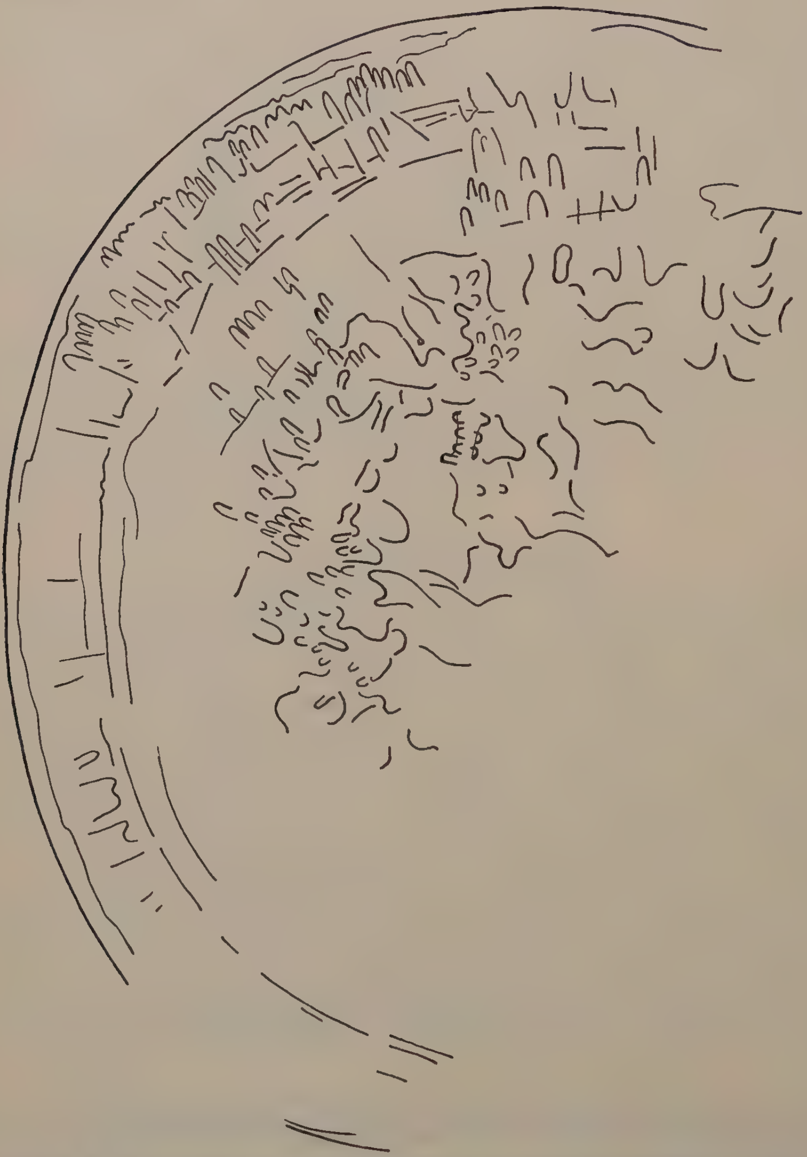


Text-fig. 4. *S. subechinata*, conjugated filaments and zygospores.

I have had this species from two localities in Essex and one in Kent. In contrast to the species previously described, the cells tend to be longer, sometimes much longer, than broad. Pl. 51, fig. 4, shows the appearance of the filament, and Text-fig. 1*c* is a camera lucida drawing of the chloroplast, showing the rather marked central rib seen on occasion but I am not certain if this character is constant. The chloroplasts in Pl. 51, fig. 4, are somewhat changed in appearance; this change accompanies the onset of the conjugating state. They become shorter, thicker, deeper green and make fewer turns round the cell.

All cells of the filament conjugate; the zygospores typically have blunt rounded ends as shown in Text-fig. 6 and Pl. 51, fig. 4, though occasionally there is a tendency to a more ovoid shape (Text-fig. 7). The colour which can be seen in them is almost entirely due to the oily contents; when this is pressed out, the membranes of the zygospore are seen to be of the palest yellow, almost colourless.

The nucleus has, unlike the preceding species, an almost spherical shape; it is rather well characterized by this, by the absence of chromocentres and by the striking appearance of the nucleolus (Text-fig. 8*a*; Pl. 52, figs. 4–6). In the latter, the organizer tracks are well marked off from the rest of the nucleolus, whose substance stains less deeply. They usually make only one or two turns round it; sometimes an apparent forking is seen. During the onset of mitotic prophase these tracks may occupy a greater proportion of the nucleolus, and the substance within them by now, if not already at resting stage (Text-fig. 8*a*), is seen to be separated from the rest of the nucleolus by a number of fine concentric membranes.



Text-fig. 5. *S. subechinata*, zygospore, showing 'sub-echinate' mesospore (×1200).

The N.O. chromosomes, of which there are two, have been described at prophase stage elsewhere (Godward, 1953). Of the ten metaphase chromosomes, the two N.O. chromosomes are long, three are of medium length and five short (Text-fig. 3*f*). All appear to have localized centromeres of the normal type, since at anaphase the chromatids are aligned with the spindle (see Text-fig. 3*e*, and also Godward (1954)). The nucleolar substance has a tendency to lie around after the dissolution of the nucleolus in the form of blobs and membranous structures; ultimately it becomes an equatorial mass in the spindle, surrounding the chromosomes and subsequently the chromatids, as described elsewhere. Late anaphase has a striking appearance, which is, however, not confined to this species. At each pole of the spindle lies a dense mass of nucleolar substance, completely obscuring the chromatids; from the mass two horns project in the direction of the equator; these indicate the position of the N.O. chromosomes as described elsewhere (Godward, 1953). Pl. 52, fig. 3, shows this anaphase stage; only one of the two horns at each pole is in focus. Cytologically, therefore, the species exhibits a number of remarkable features and those most likely to be seen in a rapid investigation are the resting nucleus, side view of full metaphase, and anaphase.

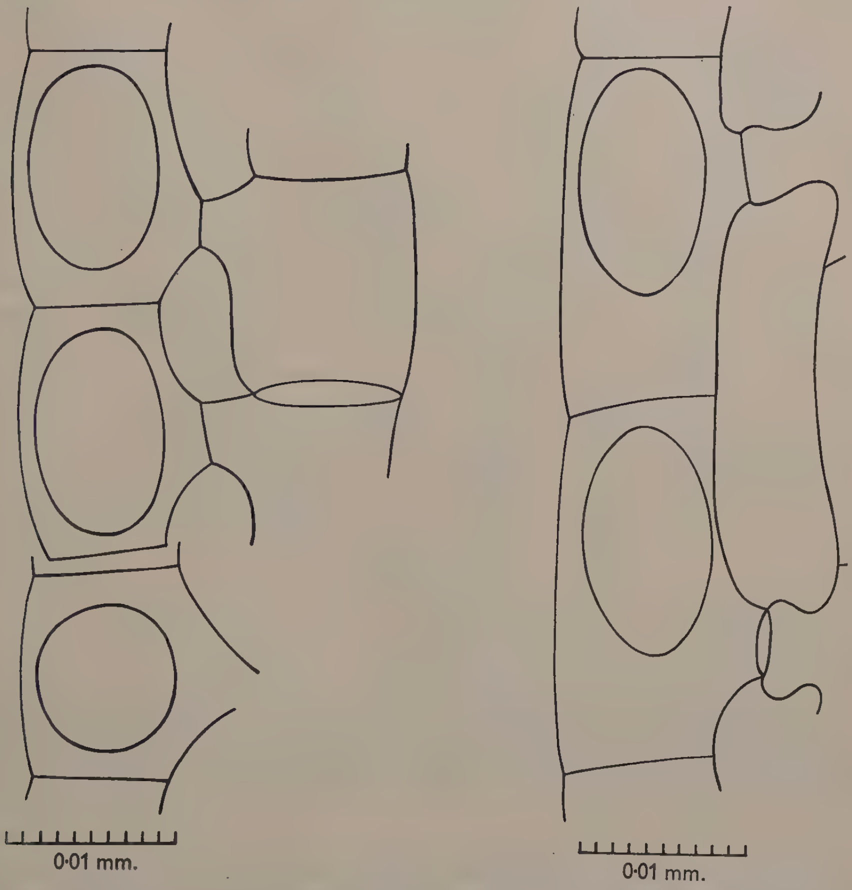
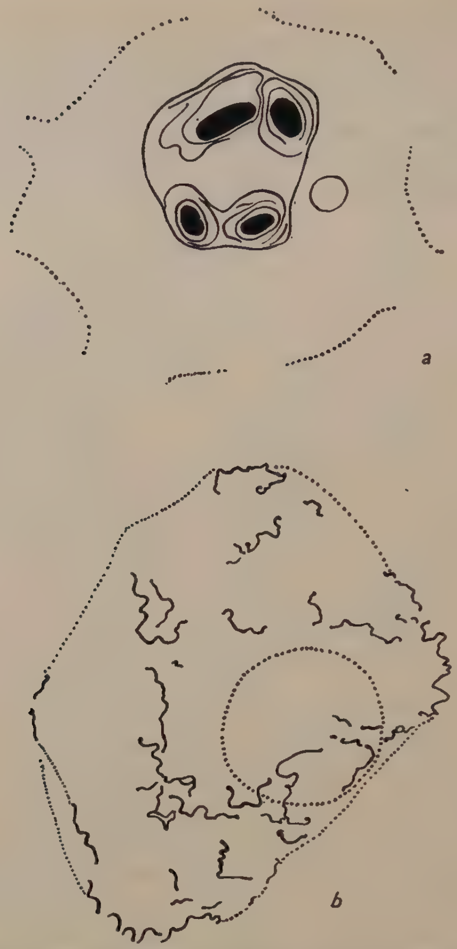


Fig. 6. Fig. 7.

Text-figs. 6, 7. *S. britannica*, conjugated filaments and zygospores (× 220).



Text-fig. 8. (*a*) *S. britannica* resting nucleus, showing nucleolus with organizer tracks surrounded by membranous structures. A small sphere of unorganized nucleolar material lies outside the nucleolus (×1600). (*b*) *S. subechinata*, resting nucleus, showing thread-like chromocentres peripheral in the nucleus (×2000).

Comparison with other species

If *S. britannica* could have been referred to an existing species it would most probably have been to *S. nitida* or perhaps *S. neglecta*. Investigation of the history of *S. nitida*, the search for authentic herbarium material or even an authentic description, has revealed a state of affairs so unsatisfactory that it is felt the specific epithet '*nitida*' should most probably be rejected. It has become in fact a label for various forms more or less resembling each other.

Conferva nitida Dillwyn 1809 is represented very inadequately by a description with figures, which give no information about the zygospores, and these data are usually accepted as the basis for *Spirogyra nitida*. It is, however, erroneously so assigned. *Spirogyra nitida* (O. F. Müller) Link was originally described as *Conferva nitida* O. F. Müller in *Fl. Dan.* 5, 7 tab. 819, 1782. The description is very inadequate ('*Conferva* nitida *filamentis simplicibus, longis articulatis*') and the figure shows no reproductive stage. The type material could not be traced amongst specimens kindly sent from the Botanical Museum, Copenhagen.

In the published descriptions, there seems considerable confusion about the dimensions of *S. nitida.* Müller (1782) apparently does not give any dimensions. Dillwyn (1809) figured three filaments, one 4·5 mm., the others 3 mm. wide, describing them as 'magnified 1'. In Kützing (1843) two filaments, one 8·5 mm., the other nearly 9 mm. wide are described as '300 mal vergrössert' which I take to give the actual width of the cell as about 30 μ. In Kützing (1855) a filament 17 mm. wide is described as × 300, giving it an actual width of about 57 μ (the zygospore is shown considerably narrower). Kützing (1863) says the sterile cells are 1/36–1/30, seldom 1/28‴ thick; Rabenhorst (1868) says the cells are 36–28‴ (presumably 1/36–1/28‴ was intended) equal to 0·0024–0·0031‴ thick, which I take to be about 76 μ; this is approximately the width attributed to *S. nitida* in all later works. Borge (1913) gave it as 60–110 μ, but Kolkwitz & Krieger (1941) restricted its range to 70–89 μ as a result of their transfer of *S. principes* (Vauch.) Cleve, which had been accepted as a synonym of *S. nitida* by every author from Kützing (1843) onwards, to *S. setiformis.* The zygospore was not seen by Müller (1782) or Dillwyn (1809), although Vaucher (1803) observed, and drew a zygospore for *S. princeps* (as *Conjugata princeps*) a specific name subsequently regarded as a synonym for *S. nitida.* Kützing (1843) figured *S. nitida* in 1863 referring to the 'spores' as elliptic, a description followed by later authors. Petit (1880) described the zygospores as elliptical with attenuated ends, yellowing on maturity. Borge (1913) described the 'membrane' of the zygospore as chestnut brown and smooth, while Kolkwitz & Krieger (1941) refer to the thick smooth brown mesospore. Except for those of Petit, all the figures are small, mostly showing the ends of the zygospore rounded to a greater or lesser degree, and do not altogether confirm the accompanying descriptions. Czurda (1932) remarked 'Keine geeignete Figuren vorhanden', which may have led Kolkwitz & Krieger (1941) to adopt for *S. nitida* a figure originally described as of *S. szechwanensis* by its author (Jao, 1935). This figure shows a dehiscence line in the zygospore, a character not hitherto found in any description or figure of *S. nitida.*

It seems to me that Czurda was certainly justified in regarding *S. nitida* as an imperfectly described species.

Of the more recent accounts of it, that of Borge (1913) is the only one giving dimensions as great as those of *S. britannica.* The latter species differs from Borge's interpretation of *S. nitida* in the more rounded zygospore, the pale colour of the mesospore, the content of brown oil in the zygospore, and the number of turns of the chloroplast in the cell reaching six instead of being limited to two.

Examination of specimens named as *Spirogyra nitida* in the British Museum, Cambridge, Kew, and Stockholm Herbaria showed that these were heterogeneous and represented a number of different species.

The cytology of *S. neglecta* and of *S. nitida* has been the subject of investigation early in the present century. Tröndle (1911), in his classic paper on meiosis in *S. neglecta,* gives a chromosome count of 12. He figures 12 small chromosomes of equal size. Berghs (1906) gives a count of 12 for *S. nitida,* and in three comprehensive plates gives a great deal of information about every stage of mitosis. In regard to the position of the centromere, and the distribution of nucleolar substance (N.S.) at metaphase and anaphase, I could match his figures with similar ones from *S. britannica.* The presence of two 'horns' on his anaphase plates indicates, as in *S. britannica,* the presence of two N.O. chromosomes. However, this type of distribution of N.S., and the presence of two N.O. chromosomes, are the commonest characters in the genus. (I do not intend to discuss Berghs's necessarily tentative interpretation of his figures.) Neither Tröndle nor Berghs has observed the features of the nucleolus found in *S. britannica.* Their chromosome counts of 12 equal-sized small chromosomes contrast with the 10 chromosomes, two long and N.O., three of medium length, and five small, characteristic of *S. britannica* and found in all the collections from three different localities. *S. britannica* is particularly well characterized cytologically. Yet when it is remembered that these earlier investigators sectioned wax blocks, and when it is noted that their figures show sometimes more, sometimes less than 12 chromosomes, indicating cutting up of, and cutting away of, chromosomes, by the microtome knife, it is still possible that they did have material with the 10 chromosomes as described above.

The material used by the above investigators was unfortunately not clearly referable to *S. nitida*. Thus Tröndle says that his species with cells 44–50 μ broad and zygospores 80–100 μ long, was a form 10–15 μ thinner than the type of *S. neglecta*, itself thinner than *S. nitida*. Berghs says: 'Nous devons faire remarquer que nous ne sommes pas parvenus, à l'aide des Systématique que sont à notre disposition, à déterminer avec certitude l'éspèce de *Spirogyra* que fait l'objet de ce travail. Nous pouvons dire seulement que notre *Spirogyra* resemble assez bien au *S. nitida*.' He gives no other information whatever about the morphology of his species.

It seems to me there is no reasonable alternative but the establishment of *S. britannica* as a new species, in which the well-defined cytological characters are linked to the clearly stated morphological ones that have been found in the cytologically studied material.

If a little speculation may be permitted, I would add that if one adds the characters of *S. neglecta* to those of *S. nitida*, as they are given by Kolkwitz & Krieger (1941), the resulting combination covers most of the descriptions and herbarium specimens of *S. nitida* though not all. It is still a heterogeneous collection of forms, but one may doubt if the specific epithet *neglecta* has any better basis than *nitida*.

NOTE ON THE METHOD OF STAINING

This has already been described (Godward 1950*a*) in full. Briefly, the living threads are placed in a mixture of three parts of 95 % alcohol with one part of glacial acetic acid, freshly mixed. When decolorized, they are, one by one as required, transferred to water and then to a concentrated aqueous solution of iron alum, and again back to several changes of water. The time in each of these fluids is not more than a minute. A thread is then placed on a slide in a drop of acetocarmine (a saturated solution of carmine in 45 % acetic acid), a cover-glass (number 0) placed over it, and the preparation carefully heated over a spirit lamp or lamp-shade; boiling usually does no harm, but more carmine must be added if the solution tends to dry up. A piece of blotting-paper is then laid over the cover-glass and the preparation gently pressed, a familiar procedure in the ordinary acetocarmine squash methods as used with angiosperm or animal material. If overstained, the preparation may be differentiated with 45 % acetic acid. To make the preparation permanent, it is only necessary to put the slide into a vessel containing the fixing fluid (three parts 95 % alcohol to one of glacial acetic acid), leaving it till slide and cover-glass come apart, then recombine them with a drop of Euparal. It is better to wash off the acetic acid first, by passing slide and cover-glass rapidly through absolute alcohol, before putting on the Euparal. Flat smearing dishes are the most convenient vessels; they should be provided with glass sheets as covers. The slide is then laid, cover-glass down, supported at the ends by the two raised portions of the floor of the dish.

NOTE ON THE IMPORTANCE OF THE PERMANENT PREPARATION

Since the cytological data form part of the diagnosis of the species, the permanent preparation has the same importance as the herbarium specimen; it is part of the type material. Where extreme difficulty is encountered in the process of making the preparation permanent, a photograph of the temporary mount, the untouched negative of which should be available for inspection, might be added to the unsatisfactory permanent preparation, and the whole regarded as type material.

In the hope that it will prove practicable to do so, every effort will be made to provide such type material for *Spirogyra*.

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EXPLANATION OF PLATES

PLATE 51

Fig. 1. *S. submargaritata*. Conjugated filaments and zygospores, with part of a vegetative filament (×170).

Fig. 2. *S. subechinata*. Conjugated filaments and zygospore (×130).

Fig. 3. *S. subechinata*. Conjugating filaments. Note the larger size of the 'female' gametangium, the altered cell contents of the gametes, the shape of the conjugation canal, and the interruption of the fertile by intervening sterile cells (×120).

Fig. 4. *S. britannica*. Conjugated filaments and zygospores. Altered contents are seen in the cells of all the conjugating material (×130).

PLATE 52

Fig. 1. *S. submargaritata*. Resting nucleus, showing 4 nucleoli (the maximum number) and chromocentres (×2700).

Fig. 2. *S. submargaritata*. Part of the anaphase nucleus shown in Text-fig. 3*a*. Only the uppermost metaphase plate is in focus, with one or two chromatids from the lower plate. The chromatids are disposed on a flat plate as at metaphase, though the anaphase plate is of rather smaller diameter; it is occupied by nucleolar substance in which the chromatids are embedded (×2700).

Fig. 3. *S. britannica*. Anaphase. The attenuated and (in this photograph) invisible chromatids are aligned longitudinally with the spindle and not flat with the plate as in the preceding species. They are surrounded with a thick coating of nucleolar substance, which marks their position. At each pole is seen one of the two projecting 'horns' which are present there, the other being out of focus. These 'horns' show the position of the longest (N.O.) chromatids, which hang back farthest (×3000).

Figs. 4–6. *S. britannica*. Three nucleoli, showing some of the forms taken by the organizer tracks—the deeper staining regions—in the nucleolus. Nucleolar material external to the track stains more palely, and there is some indication in the photographs of membranous layers surrounding the track material at its junction with the external material (cf. Text-fig. 8*a*) (×3000).

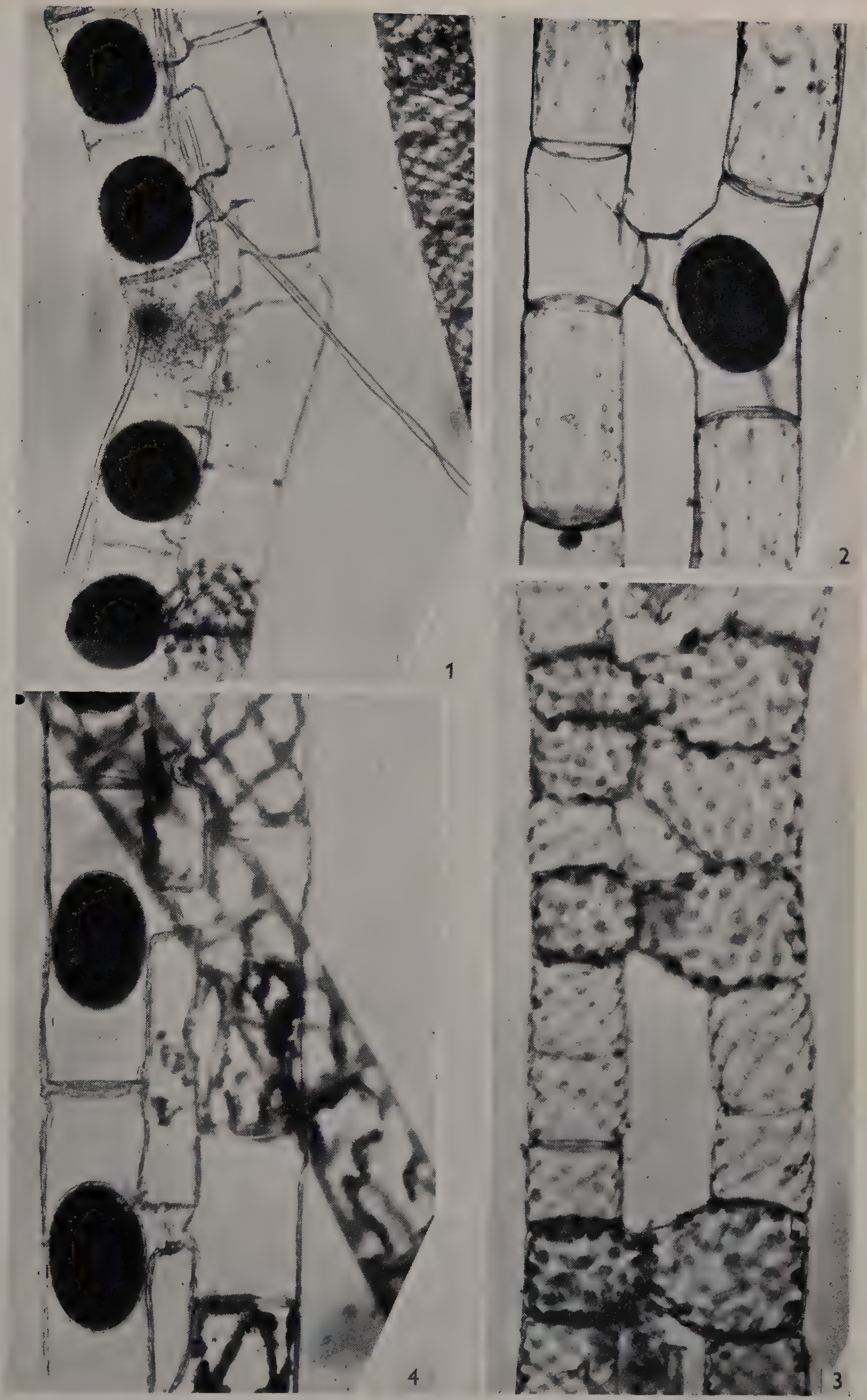
PLATE 53

Photographs of the mesospore of *S. subechinata* at different local levels (×1200).

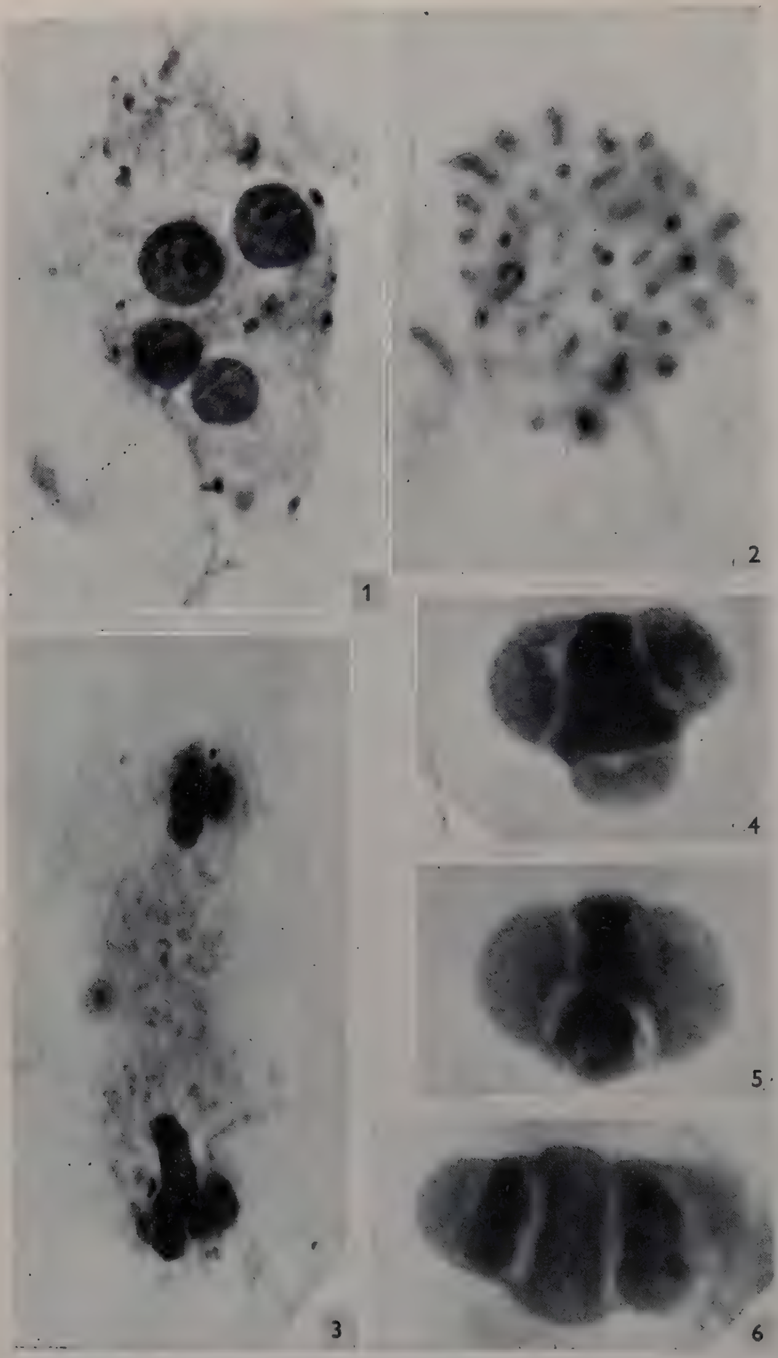
Fig. 1. Surface of mesospore, showing tips of projecting rods.

Fig. 2. Lower levels of the mesospore, showing the wide network with irregular lacunae; on the network the rods are erected.

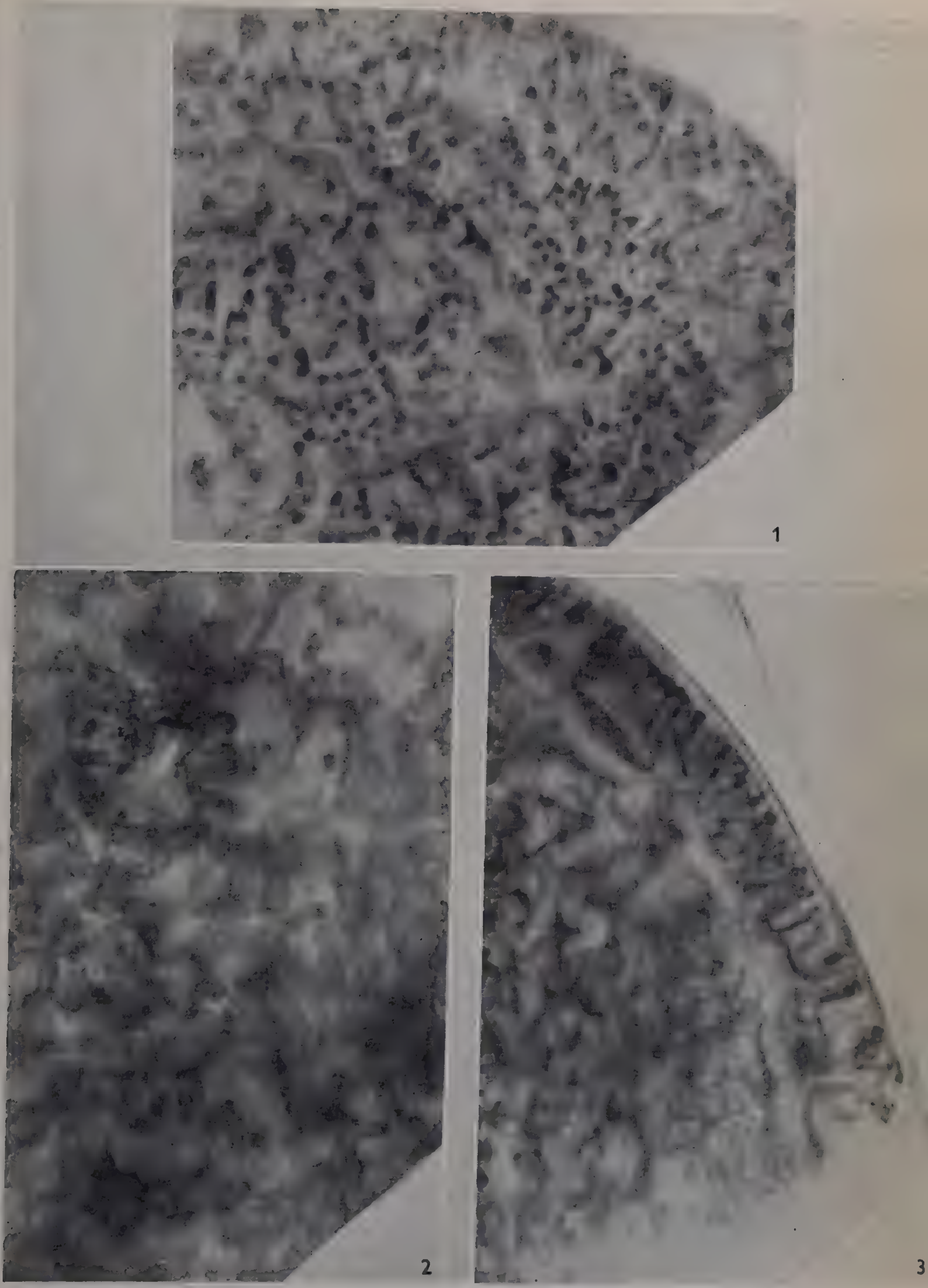
Fig. 3. Optical section of the mesospore, showing the structure in depth. The rods can be seen arising from the inner level of the mesospore; they occupy most of the thickness of the membrane, but do not project beyond its outer surface. The exospore is smooth, distinct, separated from the mesospore by a small space.



1, *Spirogyra submargaritata;* 2 and 3, *Spirogyra subechinata;*
4, *Spirogyra britannica.*



1 and 2, *Spirogyra submargaritata*; 3, 4, 5 and 6, *Spirogyra britannica*.



1, 2, and 3, *Spirogyra subechinata.*

Studies in the systematic anatomy of the Zingiberaceae. By P. B. Tomlinson.

(Communicated by Dr C. R. Metcalfe)

(With 10 Text-figures)

[Read 19 January 1956]

Introduction

The object of this paper is to give a description of the vegetative anatomy of the Zingiberaceae with reference to the taxonomy of the family. The first studies on the subject were made by pharmacognosists working on the officinal rhizomes, and their early observations are summarized by Futterer (1896). Later work was also concentrated on the underground parts, and the first general anatomical examination of representatives of the family was made by Petersen (1893), followed by Futterer's own observations. Schumann (1904) includes notes on the anatomy of the Zingiberaceae in the *Pflanzenreich*, but again is mostly concerned with the rhizome. In the second edition of the *Naturlichen Pflanzenfamilien*, Loesner (1930) includes a brief summary of the anatomy of the family without adding any original data. The most comprehensive work, presenting a collation of existing knowledge and much original information, is found in the section dealing with the Zingiberaceae in Solereder and Meyer's *Systematische Anatomie der Monokotyledonen*. Anatomical notes on eighteen genera and some seventy species are included. Except for isolated scraps of information there has been no subsequent work on the descriptive anatomy of the family.

The present study is based on that in Solereder & Meyer (henceforth to be referred to as S. & M.), whose work is confirmed and extended, with special attention to certain taxonomic aspects to which S. & M. did not give any emphasis. Since a complete bibliography and summary of the literature is included in the account in S. & M., in several instances no reference is here made to original papers. Also several of these early publications were inaccessible.

General morphology

The Zingiberaceae are a monocotyledonous family of perennial, mostly rhizomatous herbs. The usually fleshy rhizome is sympodially branched, each branch ending in an erect shoot bearing leaves, flowers or generally both. New branches develop from buds in the axils of scale leaves at the base of the erect shoot. These renewal buds may grow downwards some distance before finally turning upwards, e.g. *Curcuma domestica*, or more frequently their preliminary elongation is horizontal. In *Costus macranthus* the rhizome grows vertically downwards and remains in this position to act as a storage organ. The rhizome may be short or long, stout or thin, and is covered with distichously arranged scale leaves with an encircling insertion. The rhizome is composed generally of distinct segments, each one being the persistent, basal, scale-leaf bearing part of a branch, before it turns up as an erect shoot. The rhizome therefore is built up from the increments of many years' growth.

Roots are borne on the rhizome only. They may be slender, but are often thick and fleshy, spindle-shaped (*Globba*) or with tuber-like distal thickenings (*Curcuma*). Some functional differentiation between prop-roots, storage roots and feeding roots may occur.

Two contrasting types of organization are found in the erect leafy shoots in the family (Fig. 1). Those of the section Zingiberoideae show a typical monocotyledonous construction, being unbranched and composed of a pseudo-stem of closely compacted concentric sheaths within which the true stem extends to a variable height (Fig. 1a).

In these the leafy shoot may reach a length of up to 5 m. The true stem, on the other hand, may be very short, e.g. *Kaempferia*, where no internodal extension has occurred. The distichously arranged leaves have sheaths which are open on the side opposite the lamina insertion, although the two margins may overlap to some extent. At the junction of lamina and sheath is a ligule of varying size. The sheaths are long, the lowest ones bear only a rudimentary lamina, whilst at successively higher nodes the shape and size of the lamina increases until the typical form of the foliage leaves is achieved. Lamina and sheath may be distinct where a long or short petiole is developed; often, however, this is absent and the leaf blade is gradually confluent with the sheath. In some species, e.g.

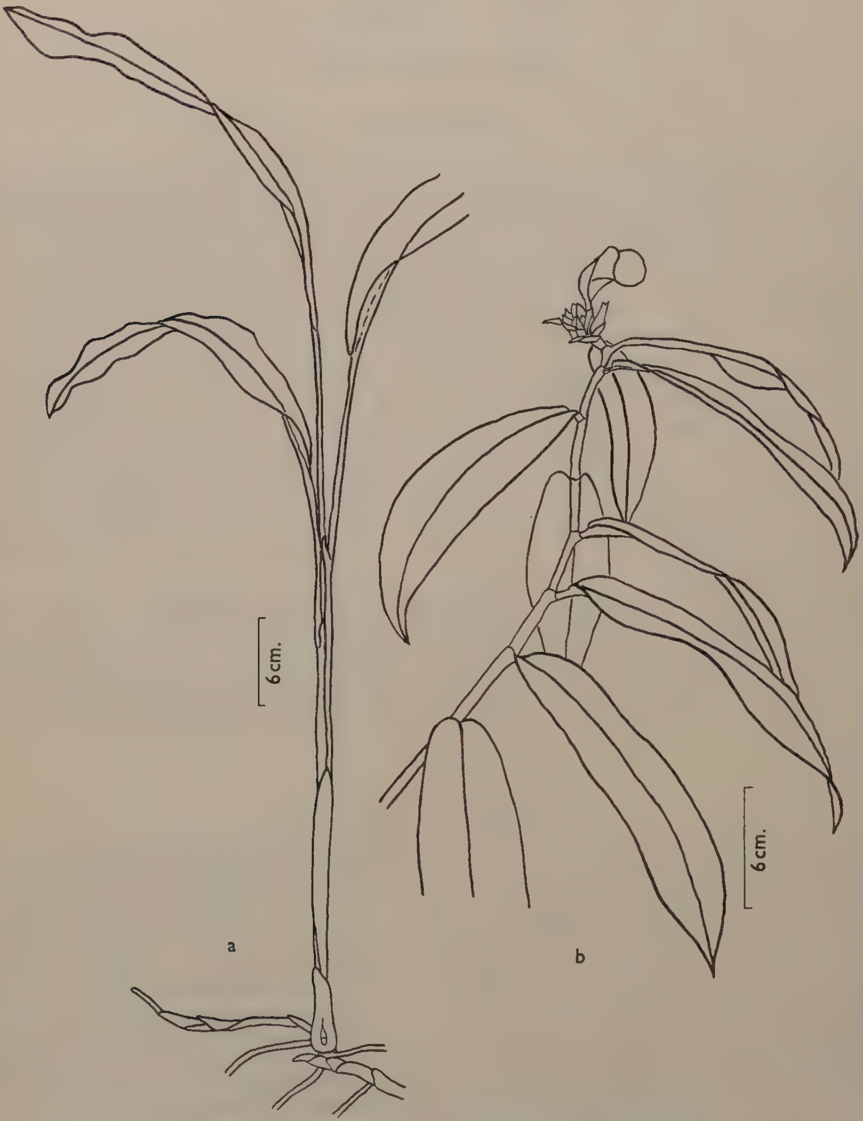


Fig. 1. (After Holttum, 1950.) (a) *Elettariopsis curtisii*, rhizome ending in a leafy shoot; illustrating the habit of the Zingiberoideae. (b) *Costus speciosus*, top of flowering stem; illustrating the habit of the Costoideae.

Kaempferia, the base of the lamina is only distinguished from the sheath by the position of the inconspicuous ligule.

The members of the section Costoideae, on the other hand, differ from the rest of the family in showing a vegetative organization that is unique among flowering plants (Fig. 1 b). In place of the distichous arrangement of leaves described above, a peculiar spiral phyllotaxis (spiromonostichy) is developed with divergences down to one-eighth or less, when the spiral becomes very steep. The true stem is well developed, elongated and persistent, often straggling and frequently branched, the branches breaking through the leaf sheaths. The sheaths are entire, tubular to the apex and generally short with the petiole articulate to the top of the sheath. The leaves are said to be deciduous. The ligule is represented by a complete though usually narrow ring, which may be split by subsequent growth of the stem.

Throughout the family the leaf lamina is simple and the margin entire. The lamina is never very small and has a maximum length of about 1 m. In shape it is most commonly lanceolate and sometimes it is cordate at the base. The lamina may be unequally developed on the two sides of the midrib and the difference is most conspicuous at its base.

The erect inflorescence is terminal, either on a leafy shoot or on a separate leafless shoot. According to Holttum (1950) the inflorescence consists essentially of an axis bearing spirally arranged primary bracts, each of which subtends a flower-bearing cincinnus. A valuable description of floral morphology in the Zingiberaceae is given in Holttum's paper.

Taxonomy of the family

In Bentham and Hooker's *Genera Plantarum* the Scitamineae as a whole were considered to be one family included within the second series Epigynae. Subsequently, the Scitamineae were elevated to a distinct order by Engler and Prantl in the first edition of *Die Naturlichen Pflanzenfamilien* and divided into four families: the Musaceae, Zingiberaceae, Cannaceae and Marantaceae. Later on the Lowiaceae and Strelitziaceae were separated from the Musaceae by Hutchinson (1934).

Schumann (1904) divided the Zingiberaceae into two subfamilies, the Zingiberoideae with many genera and the Costoideae with four genera. These subfamilies are very distinct vegetatively:

Zingiberoideae—leaves arranged distichously, sheaths open, lateral staminodes large, small or rarely none, stylodes (nectar glands) various, always more or less columnar, rarely absent. Plants aromatic.

Costoideae—leaves arranged spirally with divergences of the order 1/5, 1/6, 1/7, etc., sheaths completely tubular or later split by the outgrowth of a branch, stylodes absent, nectar glands represented by structures embedded below the base of the flower tube. Above-ground parts of the plant not aromatic.

The Zingiberoideae are further subdivided:

(1) Lateral staminodes petaloid, free from the labellum.
  Ovary unilocular with parietal placentation. Tribe *Globbeae*
  Ovary trilocular with axile placentation or unilocular but with basal or free columnar placentation. Tribe *Hedychieae*
(2) Lateral staminodes never petaloid, small or absent. Tribe *Zingibereae*

While the tribe Globbeae appears to be a natural group, Holttum questions the arrangement of the remaining two tribes, for as Schumann himself was aware, *Zingiber* itself has a petaloid development of the staminodes, although this is obscured by their fusion with the labellum so that they appear as two lateral lobes of a 3-lobed structure.

Therefore, in a proposed revision of the family, Holttum transfers *Zingiber* to the Hedychieae, the remaining tribe becoming the Alpinieae which is equivalent to

Schumann's Zingibereae without *Zingiber*. Evidence will be quoted later in support of Holttum's arrangement.

The present conception of the family therefore is:

Zingiberaceae (47 genera and about 1400 species)
  Costoideae (Schum.), subfamily 1
  Zingiberoideae (Schum.), subfamily 2
    Globbeae (Schum.), tribe 1
    Hedychieae (Holtt.), tribe 2
    Alpinieae (Holtt.), tribe 3

The account of the anatomy of this family deals largely with differences between the subfamilies Costoideae and Zingiberoideae, and where the differences are large the structure of these two groups will be described separately.

Since Holttum's work deals only with the Zingiberaceae of the Malay Peninsula his solutions to many problems within the family are only partial, and he indicates how incomplete is our knowledge of the family. Holttum emphasizes the importance of using the various modifications of the inflorescence for delimitation of the genera. Considering the primitive zingiberous inflorescence to be terminal on the leafy shoot and to consist of cincinni in the axils of primary bracts with a tubular secondary bract or bracteole at the base of each new branch of a cincinnus, the genera *Hedychium* and *Alpinia* are suggested as the most primitive members of their respective tribes, with some relationships between the two. Vegetatively, plants of the *Alpinia*-tribe are generally larger than those of the *Hedychium*-tribe in which the leafy shoot tends to have rather a short stem with a small number of more erect leaves, often on fairly long petioles and with the length of the sheath much less than that of the petiole and blade. Only *Elettariopsis* of the Alpinieae has this habit (Fig. 1a).

GEOGRAPHICAL DISTRIBUTION, ECOLOGY AND ECONOMIC USES

According to Loesner (1930), in the Zingiberoideae, the Globbeae and Hedychieae are more or less confined to the Old World. The Globbeae are entirely Asiatic. In the Hedychieae, only *Hedychium coronarium* extends to America, while species of *Kaempferia* occur in Africa. In the Alpinieae species of *Renealmia* occur frequently in America, while *Aframomum*, *Renealmia* and two species of *Aulotandra* are found in Africa. The centre of distribution of the Zingiberoideae is, however, in Indo-Malaya.

The Costoideae, on the other hand, show a very different pattern of distribution, and appear to be centred in Central America. The monotypic *Monocostus* and oligotypic *Dimerocostus* are confined to Bolivia, Peru and Panama. *Costus* has a pan-tropical distribution, although the majority of its species are concentrated in Africa and especially America. The remaining genus *Tapeinochilos* extends from the islands of Ceram and Aru, through New Guinea to Rockingham Bay in Queensland.

Ecologically, as far as Malaya is concerned, the species of the Zingiberaceae are characteristic of the ground flora of the primitive forest where they are very common and most abundant in lowland districts. Few species are able to withstand direct exposure to the sun.

Members of the Zingiberaceae find wide application in commerce as spices and condiments; several species are officinal. Gingers of various types are derived from *Zingiber officinale* and other *Zingiber* spp. The high starch content of their aromatic rhizomes enables other species to be used as food, comparable to the related arrowroot (*Maranta arundinacea*). Turmeric, a yellow colouring matter, is obtained from *Curcuma domestica* and other *Curcuma* spp. Other members of the family are used as dyes and perfumes; the fibres of *Alpina speciosa* have been used commercially; the stems and sheaths of

Phaeomeria hemisphaerica and *Hedychium coronarium* when flattened and dried form a writing material. Many members of the family find a local use as native foods, medicines and flavourings for which they are cultivated as village plants, often escaping and establishing themselves on waste ground (Holttum, 1950).

MATERIAL AND METHODS

In the present investigation, which deals with the vegetative parts only, material of forty-one species belonging to twenty genera was available. Six of these genera and twenty-six of these species are not mentioned by S. & M. The main sources of material were the greenhouses of the Royal Botanic Gardens, Kew, supplemented by pickled material of wild plants from Malaya, supplied by Prof. R. E. Holttum. In some species only the aerial parts were available.

The following species were studied:

List of species studied

Subfamily Costoideae

Costus afer Ker-Gawl., *C. discolor* Rosc., *C. lucanusianus* J. Br. et K. Sch., *C. malortieanus* Wendl., *C. rumphianus* Valet. ex Heyne, *C. tappenbeckianus* J. Br. et K. Sch.

Subfamily Zingiberoideae

Tribe Globbeae

Globba bulbifera Roxb., *G. winniti* C. H. Wright.

Tribe Hedychieae

Brachychilum horsfieldii O. G. Peters, *Camptandra ovata* Ridl., *Cautleya spicata* Bak., *Curcuma domestica* Valet., *Curcuma* sp., *Hedychium coccineum* Buch. Ham. ex Sm. var. *angustifolium*, *H. elatum* R. Br., *H. gardnerianum* Rosc., *H. malayanum* Ridl., *Kaempferia angustifolia* Rosc., *K. gilberti* Hort., *K. kirkii* (Hook.) Witt. et Per., *K. rotunda* L., *Roscoea cautleoides* Gagnep. var. *grandiflorum*, *R. humeana* Balf. et Sm., *R. purpurea* Sm., *Scaphochlamys breviscapa* Holtt., *S. erecta* Holtt., *S. rubromaculata* Holtt., *Zingiber officinale* Rosc.

Tribe Alpinieae

Aframomum sp., *Alpinia javanica* Bl., *A. sanderae* Hort., *A. speciosa* K. Sch., *Burbidgea schizocheila* Hort., *Catimbium latilabre* (Ridl.) Holtt., *C. speciosum* (Wendl.) Holtt., *Elettaria cardamomum* Maton., *Elettariopsis curtisii* Bak., *Geostachys taipingensis* Holtt., *Hornstedtia conica* Ridl., *H. scyphifera* (Koenig) Stend., *Renealmia* sp.

Material was fixed in formalin-acetic alcohol and washed well in water before sections were cut. Sections were mostly cut from unembedded material on a Reichert sliding microtome at thicknesses varying from 15 to 100 μ, mostly at 30 μ. Leaves of a few species were embedded in paraffin wax and sectioned on a Cambridge rocking microtome.

All sections were examined:

(i) Unstained and mounted in glycerine.

(ii) Stained with Sudan IV to determine the distribution of suberin and cutin.

(iii) Stained in phloroglucinol and concentrated hydrochloric acid to determine the distribution of lignin.

(iv) After clearing in 'Parozone', a commercial chlorine bleaching agent.

(v) A number of permanent preparations were made from cleared sections stained in safranin and Delafield's haematoxylin and mounted in Canada balsam.

Surface preparations of the epidermis, to which the hypodermis often remains attached, were made by stripping off the epidermis. When this was not possible, unwanted tissue was scraped away from a strip of leaf laid flat on a slide. Leaves that did not respond readily to this scraping treatment were immersed in 70 per cent sulphuric acid in a hot oven for several hours which removed the epidermis. These preparations were examined unstained and stained as above.

For the detection of oil cells two techniques were used:

(1) When cleared sections were treated with 10 per cent potassium hydroxide solution, washed in water and mounted in chlor-zinc-iodide, the suberized walls of the oil cells showed a bright yellow colour in contrast to the blue of the normal cellulose of surrounding cell walls.

(2) The standard technique used for the demonstration of oil cells: cleared sections were mounted in aqueous I_2KI (Lugol's iodine) and a drop of a 70 per cent solution of sulphuric acid was carefully drawn beneath the coverslip by means of filter-paper. With a little practice staining of the walls was achieved with a minimum of disorganization of the tissues. The oil cells were then made conspicuous by the yellow colour of their walls, whilst normal cellulose walls swell and stain blue. Continued action of the acid dissolves the cellulose, whilst the suberin lamellae of the oil cells, and other cutinized and suberized structures, remain as yellow-brown fragments.

Maceration was largely used for the study of the tracheal elements, because it is seldom possible to determine the type of element in sections. Material was macerated in 5 per cent chromic acid, in a warm oven, for a variable period of up to several days depending on the type of material. For immediate results the tissue was boiled in 10 per cent potassium hydroxide for several minutes, washed in water and treated with 20–30 per cent chromic acid for about 15 min. Preparations were examined mounted in glycerine.

ANATOMY OF THE LAMINA

Zingiberoideae

Macroscopic features. The leaves of the Zingiberoideae have a relatively uniform appearance and texture, generally thin, sometimes slightly fleshy, never leathery or coriaceous and rarely conspicuously hairy. A midrib region including several veins is developed, protruding on the abaxial surface and slightly concave on the adaxial surface. This disappears within a short distance of the base of the lamina in some species, e.g. *Camptandra* spp., or remains well developed throughout the length of the lamina. The primary longitudinal veins of the leaf run to a marginal commisure at a variable angle, joining this close to, or at some distance from, the apex. Smaller longitudinal veins are interspersed between the primary veins, and these longitudinal systems are connected by short, transverse veins. The vein system is closed, i.e. there are no free vein endings. The distance between bundles, and consequently the bundle-free area, is very variable. The veins rarely produce a conspicuous ribbing of the lamina.

Details of the external surface. The epidermis was studied in surface view from the strips, the preparation of which was described on p. 551.

The epidermal cells of the adaxial surface are rectangular, or more or less hexagonal in shape, with straight walls (Fig. 2b). They are usually transversely stretched, i.e. perpendicular to the longitudinal veins, rarely they are longitudinally stretched (*Kaempferia* spp.). In size they range from $90 \times 50\,\mu$ in *K. angustifolia* to $13 \times 35\,\mu$ in *Alpinia speciosa.* Different species of the same genus show different epidermal cell sizes, e.g. *Globba bulbifera* $18 \times 24\,\mu$, *G. winniti* $30 \times 60\,\mu$; *Hedychium malayanum* $47 \times 63\,\mu$, *H. coccineum* $23 \times 50\,\mu$. The cell files, parallel to the longitudinal veins, are generally very regular and distinct.

In contrast the cells of the abaxial epidermis are much more variable and irregular in shape and size; often they are not, or only slightly, transversely stretched, whilst the walls are more frequently curved though never wavy (Fig. 2a, d). Generally the cells of the abaxial surface are slightly smaller than those of the adaxial surface. The cell files are almost always less regular and sometimes they are obscure, as in *Scaphochlamys* (Fig. 2c).

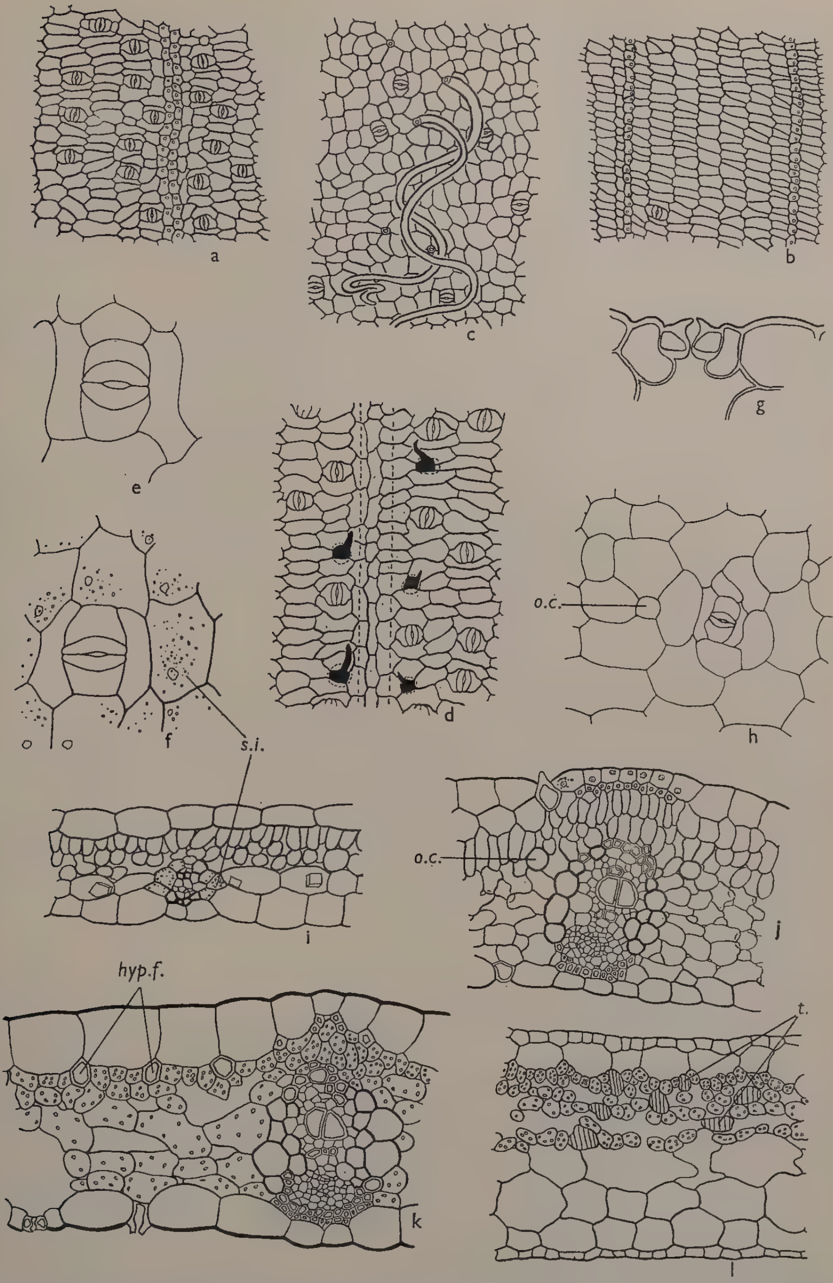


Fig. 2. (a) *Catimbium latilabre*, lower epidermis (×70). (b) *C. latilabre*, upper epidermis (×70). (c) *Scaphochlamys erecta*, lower epidermis (×75). (d) *Hornstedtia conica*, lower epidermis (×117). (e) *Costus lucanusianus*, stoma from lower epidermis (×327). (f) *Alpinia speciosa*, stoma from upper epidermis (×327). (g) *Hedychium gardnerianum*, transverse section (t.s.) stoma, upper epidermis of lamina (×377). (h) *Camptandra ovata*, lower epidermis, stoma and oil cells (×103). (i) *Globba bulbifera*, t.s. lamina (×147). (j) *Renealmia* sp., t.s. lamina, bundle of first order (×117). (k) *Elettariopsis curtisii*, t.s. lamina (×117). (l) *Scaphochlamys breviscapa*, t.s. lamina (×117). *hyp.f.*, hypodermal fibres; *o.c.*, oil cell; *s.i.*, silica; *t.*, tannin cells.

The cells above the veins on both surfaces may be modified, depending on the degree of 'buttressing' (p. 557) of the veins (Fig. 2a, b). They are generally smaller than the normal epidermal cells and are either less transversely stretched or often longitudinally extended, parallel to the vein, e.g. in *Hornstedtia conica* (Fig. 2d). In *Scaphochlamys* the bundle sheath extensions do not extend outward as far as the epidermis, and there is no differentiation of the epidermal cells above the veins (Fig. 2c).

The guard cells of the stomata are of the normal type with the long axis of the pore parallel to the veins of the first order. Four subsidiary cells are present around each stoma, two lateral and two terminal (Fig. 2e, f), sometimes with slight irregularities. Rarely, as in *Camptandra ovata* (Fig. 2h), further epidermal cells are modified about the stoma. In *Scaphochlamys* (Fig. 2c) the terminal subsidiary cells are less distinct than normal. The subsidiary cells in surface view stain less intensely than the remaining epidermal cells. In transverse section the subsidiary cells are shallower than the remaining epidermal cells (Fig. 2g). The guard cells lie in the same level as other epidermal cells; only in some *Globba* spp. are they slightly sunken.

The size of the stomata is very constant for a given species; stomata of upper and lower surfaces are identical in size. *Roscoea cautleoides*, however, was exceptional in that the length of the stomata on the adaxial surface varied from 28 to 50 μ, while those on the abaxial surface were very uniform with an average length of 40 μ. For the family as a whole there was a range in stomatal length from 23 μ in *Elettaria cardamomum* to 50 μ in *Roscoea cautleoides*. Wide variation is shown between species of the same genus, e.g. *Hedychium gardnerianum* 30 μ, *H. malayanum* 43 μ. The measurements agree approximately with the results quoted by S. & M., although there is occasional wide variation. This is to be expected as stomatal size, and the size of the epidermal cells in general, is sensitive to changes in habitat.

Stomata are generally much more frequent on the abaxial than the adaxial surface. In *Alpinia javanica* there were equal densities on the two surfaces, while in *Camptandra ovata* no stomata were seen on the upper surface. Possibly, however, stomata are never completely absent from the adaxial surface, although they are frequently very rare. S. & M. report some species in which the stomata are more numerous on the upper than the lower surface.

A description of other epidermal structures, e.g. hairs and oil cells, is given later (pp. 572 and 581).

The epidermis in section. The anatomy of the lamina was studied from sections taken at a standard median level, i.e. halfway between the apex and base of the lamina.

The epidermis bears a thin cuticle which, in sections treated with chlor-zinc-iodide, is often seen to penetrate to the base of the substomatal chambers. A slightly papillate cuticle was seen in *Hedychium gardnerianum*, *Kaempferia angustifolia* and *K. gilberti*. Of interest were the superficial granules or globules which stain with Sudan IV. These bodies appear scattered on the surface of the cuticle in several species, but are easily detached. Similar structures blocked many of the stomatal apertures in *Roscoea purpurea*. These granules may correspond to the 'Kugeln' noticed by Artz (1937) in *Zingiber officinale*.

The epidermal cell walls are slightly thicker than those of the internal cells, the thickest being the outermost wall which is reported to have occasionally a slight collenchymatous thickening at the angles (S. & M.). The epidermal cells above the veins are smaller and often slightly thicker-walled (Fig. 2j). In *Kaempferia rotunda* (and *Costus malortieanus* (Fig. 3c)) the adaxial epidermis is papillate.

The hypodermis. A hypodermis is a characteristic feature of the Scitamineae, although according to S. & M. this is least well developed in the Zingiberaceae.

In the Zingiberaceae a hypodermis may thus be:

(i) Completely absent, e.g. in *Alpinia javanica*, *Kaempferia kirkii* (Fig. 3h).

(ii) Present on both surfaces, e.g. in *Hedychium gardnerianum* (Fig. 3d), *Brachychilum horsfieldii* (Fig. 3l), when the upper or lower may be most strongly developed.

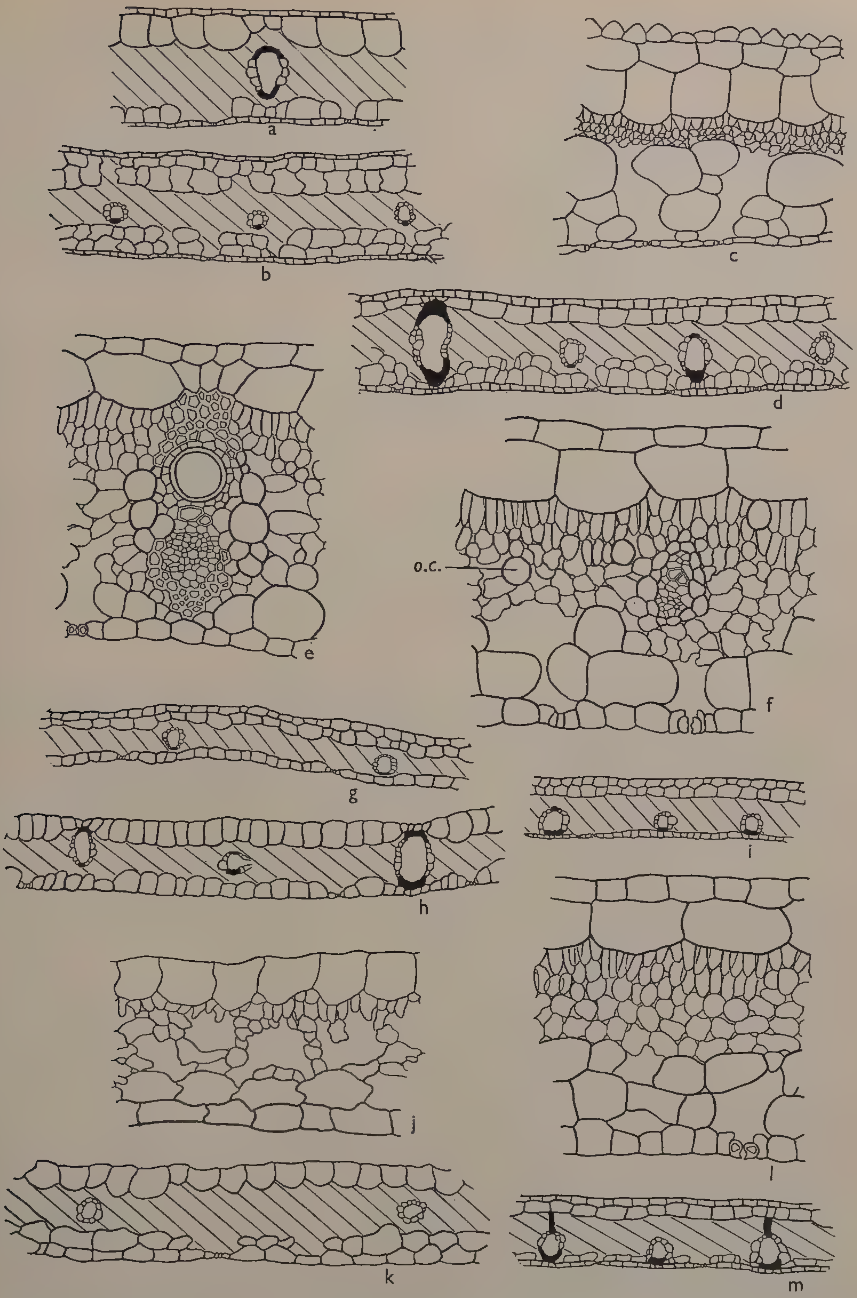


Fig. 3. All from transverse sections. (a) *Costus afer*, lamina (× 57). (b) *C. rumphianus*, lamina (× 48). (c) *C. malortieanus*, lamina (× 57). (d) *Hedychium gardnerianum*, lamina (× 48). (e) *H. gardnerianum*, lamina, bundle of first order (× 153). (f) *H. gardnerianum*, lamina, bundle of third order (× 153). (g) *Kaempferia gilberti*, lamina (× 48). (h) *K. kirkii*, lamina (× 48). (i) *Alpinia sanderae*, lamina (× 48). (j) *Camptandra ovata*, lamina (× 92). (k) *C. ovata*, lamina (× 48). (l) *Brachychilum horsfieldii*, lamina (× 153). (m) *Geostachys taipingensis*, lamina (× 48). Assimilating tissue, cross-hatched; fibrous tissue, solid black, *o.c.*, oil cell.

(iii) Present on the adaxial side alone, e.g. *Kaempferia gilbertii* (Fig. 3g).

(iv) Present on the abaxial side only, e.g. *Globba bulbifera* (Fig. 2i), *Camptandra ovata* (Fig. 3j, k).

The lateral extent of the hypodermis varies in different parts of a leaf of any one species. A hypodermis present near the midrib is less well developed towards the margin and is often absent from the margin itself. S. & M. suggest that the hypodermis has a 'water-storage' function, and it is significant that where a hypodermis is absent the epidermis itself may assume the dimensions and appearance of a hypodermis, e.g. in *Elettariopsis curtisii* (Fig. 2k), *Kaempferia kirkii* (Fig. 3h) and the adaxial surface in *Camptandra ovata* (Fig. 3j, k). S. & M. suggest that the epidermis has then taken over the function of the hypodermis.

Skutch (1930) and Löv (1926) have indicated that the hypodermal cells in the midrib are associated with leaf unrolling and act as expansion cells. In species where a hypodermis is absent from the lamina, typical hypodermal cells are present near the midrib. This is striking in *Alpinia javanica* where below the adaxial surface, on either side of the midrib, a band of typical hypodermal cells, fifteen to twenty cells wide, is developed and is very distinct from the thicker-walled ground parenchyma of the midrib and the assimilating tissue of the lamina. Hypertrophied, anticlinically extended cells are occasionally to be seen in this region in other species, and they resemble the hypertrophied cells artificially induced by Skutch (1930) in other species of the Scitamineae. According to Skutch, however, the expansion cells in *Alpinia exaltata* are at the centre of the midrib. Probably there is considerable variation in the position of the expansion cells in the group.

The individual hypodermal cells are large, more or less cubical, sometimes transversely stretched, and colourless, the only contents being occasional calcium oxalate crystals or tannin and rarely silica. A collenchymatous thickening of the wall angles is reported by S. & M. in some species. The relative size of the epidermis and hypodermis is very variable. Though the hypodermal cells are generally significantly larger than those of the epidermis, e.g. in *Hedychium gardnerianum* (Fig. 3d–f), in some species the epidermal and hypodermal cells are of a comparable size, e.g. in *Alpinia sanderae* (Fig. 3i). The epidermal cells, however, are never larger than those of the adjacent hypodermis. Although the hypodermal cells are arranged in longitudinal rows, the absence of any walls coincident with the epidermis indicates that they originate in the mesophyll and not in the dermal region.

Because stomata are infrequent on the upper surface, the adaxial hypodermis forms a more or less complete, uninterrupted layer; the abaxial hypodermis, however, is interrupted by large substomatal chambers (Fig. 3f, l). Consequently, the abaxial hypodermis, as seen through the epidermis, is irregular and the individual cells are also often irregular in shape, developing short, stout arms enclosing large intercellular spaces.

The number of hypodermal layers below a particular surface varies from one to a maximum of three. There may be differences in the size of the cells in different layers, the innermost is generally the smallest. Comparison of the number of hypodermal layers in the material examined with those quoted by S. & M. (*loc. cit.* p. 31) gives excellent agreement for any one species, and any apparent differences are probably due to the comparison of different regions of the lamina. Where S. & M. mention the actual position in the lamina, agreement is always precise. It is thus reasonable to conclude that, although there are differences in the depth of the hypodermis within a single leaf, the hypodermis in a precisely defined position in the leaf has a characteristic appearance which is diagnostic for the species. There is little constancy in hypodermal appearance at the generic or higher taxonomic level.

The mesophyll. Although the leaves I examined all show a dorsiventral structure, a 'centric' leaf structure has been recorded for *Zingiber capitatum* (S. & M., p. 32). Within the material examined there were all variations, from *Brachychilum horsfieldii*

(Fig. 3l) with a distinct 2- to 3-layered palisade and a spongy mesophyll of compact, rounded cells with little development of arms, to that shown in *Camptandra ovata* (Fig. 3j), with a scarcely distinguishable, irregular palisade with a very loose spongy mesophyll of long-armed cells. A comparison of the figures (Figs. 2i–l, 3e–f), gives some idea of the variation in extent of palisade and spongy tissues within these two extremes.

The palisade tissue is never more than three-layered and generally consists of vertically elongated, cylindrical cells, two to three times as high as wide, slightly conically pointed abaxially and compacted in varying degrees. Where the palisade consists of more than one layer, the cells of the lowest layer are the shortest, often transitional in shape to those of the spongy mesophyll below. A possible diagnostic feature for *Scaphochlamys* is the palisade-like layer of cells on the abaxial surface, in addition to that of the adaxial surface. This is best shown in thick sections and is not well marked in the figure (Fig. 2l).

The intercellular space system of the spongy tissue is in connexion with the external atmosphere via the stomata and substomatal chambers about which the air spaces are largest.

Comparison of the observations recorded by different workers for the same species suggests some variation in the structure of the assimilating tissue which would render it unreliable for diagnostic purposes. This might have been anticipated, as it is well recognized that chlorenchyma tissue in general is very plastic.

The veins of the lamina. The veins, in section, can be classified into several roughly alternating systems on the basis of size. The largest (first-order bundles) probably correspond to the basifugal, the remainder to the basipetal systems distinguished developmentally by, for example, Scott & Priestley (1925) in *Tradescantia*, and Sharman (1942) in *Zea*. Each of the largest veins has a single large xylem element and abaxially one or more small, angular xylem elements separated from the phloem group by one or two rows of small-celled conjunctive tissue (Fig. 3*e*). Extended protoxylem is found only in the largest (basifugal) bundles and even here it may appear to be absent, presumably because it becomes completely obliterated.

The bundles are sheathed laterally by one or sometimes two layers of parenchyma cells elongated parallel to the bundle. These are colourless, but may contain calcium oxalate crystals, silica or starch. The bundle sheaths are completed above and below, at least in the larger bundles, by thick-walled fibre-like cells. The extent of this fibrous or sclerotic differentiation of the bundle sheath varies with the species and the size of the bundle. The sheaths of the smaller bundles may be entirely parenchymatous (Fig. 3f); in the medium-sized bundles the fibres are generally confined to the abaxial part of the sheath (Fig. 3g, i), while in the largest bundles fibres may occur above and below and may be continued as a bundle sheath extension to form a complete buttress across the mesophyll. Often the bundle sheath extension does not reach the epidermis but remains separated by small hypodermal cells (Fig. 3m).

In *Camptandra ovata* (Fig. 3k), where the fibres of the bundle sheath are almost absent, *Burbidgea schizocheila* and the genus *Scaphochlamys*, none of the bundle sheaths extends to either epidermis, nor are the epidermal cells modified where they overlie a vein. In some other species only the larger bundles may be connected to the epidermis (Fig. 3h). In most species all bundles are connected to the abaxial epidermis, but only the largest bundles extend to each epidermis. Some *Kaempferia* spp. are exceptional in that the bundles may be buttressed to the adaxial epidermis only or to the epidermis on both surfaces (Fig. 3h). In *Geostachys taipingensis* (Fig. 3m) and *Hornstedtia* spp. the fibres are most abundantly developed and the adaxial buttress often consists of a vertical plate of thick-walled cells, which in *H. scyphifera*, in transverse section, may be one to two cells wide and up to eight cells high.

A progressive series can be arranged showing a transition of the adaxial fibres of the bundle sheath to a complete independence of the bundles. Beginning with *Hornstedtia*, described above, there follows a condition apparently characteristic of the genus *Renealmia* (S. & M., p. 33), although found in other genera as well, such as *Aframomum*. Here the adaxial fibre group of the larger bundles is independent of the rest of the bundle sheath, being separated by chlorenchyma and hypodermal cells (Fig. 2j). Finally there is the type of structure that has, as yet, been seen only in *Elettariopsis curtisii* (Fig. 2k), where, instead of a typical hypodermis, small, slightly thick-walled, colourless cells are to be found on the adaxial side at regular intervals, and occur also in the midrib. In surface view the cells are considerably elongated, simple and fibre-like. They terminate blindly or are continuous with a similar cell. These elements are apparently transitional between true hypodermal cells and the fibres of the bundle sheath. Near a vein there may be actual transitions to the true bundle fibres. This would suggest that the fibres of the bundle sheath extension are of mesophyll origin and are not derived from procambial tissue.

The modification of the epidermal cells adjacent to the veins has already been mentioned, and this change may take place where the tissues of the bundle sheath approach, but do not meet, the epidermal cells. A similar modification of hypodermal cells may occur. The hypodermis either becomes completely interrupted and replaced by mesophyll tissue which is generally more compacted than the remaining assimilating tissue, or where it is continuous, its cells are small and occasionally longitudinally extended. Occasionally the mesophyll tends to be radially arranged around the bundles. In species where the bundles are completely independent of the hypodermis and epidermis, there is no modification of these tissues or only a slight modification around the largest bundles.

The transverse veins have a very simple structure. They consist of one or two narrow xylem and phloem elements and a continuous one-layered parenchyma sheath, thick-walled mechanical elements never being present. The transverse and longitudinal bundle systems are continuous. The xylem of the transverse bundles connects with the small, last-formed elements lying between the phloem and the large metaxylem element of the longitudinal bundles.

The midrib. The structure of the midrib region was studied from sections at a standard median level. Differences between different species in the anatomy of this region are largely due to the level of divergence of the midrib bundles into the lamina. In some species, notably *Camptandra ovata*, all but one of the longitudinal veins diverge just above the base of the lamina. The midrib is therefore very inconspicuous and unthickened throughout most of the lamina, and contains a single bundle. The other extreme is represented by *Hornstedtia*, where a conspicuous thickened midrib runs along the greater length of the blade, the longitudinal veins diverging at intervals at rather obtuse angles.

The epidermis is slightly thicker-walled, smaller-celled and more papillate than that of the lamina. These features are most marked in the epidermal cells near the bundles where the latter approach the epidermis. Occasionally the midrib region is raised on the abaxial surface.

In a few instances the subepidermal ground parenchyma cells are thick-walled and conspicuously pitted, e.g. *Alpinia javanica*.

Most of the thickening of the midrib consists of the adaxial ground parenchyma. This and the ground parenchyma above the abaxial surface is continuous with the hypodermis of the lamina, and its function in unrolling the leaf has already been discussed (p. 556).

The bundles of the midrib belong to several different systems which are longitudinally continuous throughout the sheath, petiole and lamina. These systems are to be seen in section as distinct arcs, and for convenience in description the arcs have been numbered I–IV (Figs. 5, 6). Some of the arcs are either absent from, or indistinct in, transverse sections through the midrib in the median position that was selected for study, as compared with the anatomy of the petiole and sheath where the arcs are always more clearly defined. All species possess a main arc of large bundles (arc I) arranged near to the abaxial epidermis, but separated from it by at least one or two small ground parenchyma cells.

In addition, there may be arcs of smaller bundles above only (*Alpinia* spp., Fig. 6f), below only (*Globba* spp., Fig. 6a) or both above and below the main arc (*Hedychium* spp.). These subsidiary arcs are represented, at this level, by a few bundles, often one only. The bundles of the main arc (I) and of the subsidiary arcs (II and III) are often pectinated so that a single arc of alternating large and small bundles is present, e.g. in *Elettaria cardamomum* (Fig. 5e), *Roscoea* spp. (Fig. 5i). It is evident, however, that the smaller bundles in a composite arc are homologous with those arranged in distinct arcs in other species. In species in which the longitudinal veins diverge near the base of the lamina, the section of the midrib at the standard level shows a single large bundle and the midrib is not thickened at this point. Indeed, it is often slightly constricted, as in *Burbidgea schizocheila* (Fig. 5a).

The individual bundles of the main arc are of the kind which S. & M. have designated '*Musa*-type'. The earlier term Scitaminean bundle, first proposed by Rüssow (Futterer, 1896) is, however, more appropriate because of their wide occurrence in the Scitamineae. Bundles of this type are roughly pear-shaped in section and somewhat constricted across the centre (Fig. 4*a*). The abaxial half is somewhat wider, even up to twice as wide as the adaxial half.

The dominant feature is the single, large metaxylem element. Sometimes two of these appear at levels where the tapering ends of two superimposed elements overlap. Adaxial to this element is the protoxylem of one to three elements showing evidence of extension and collapse. The earliest of these protoxylem elements may be obliterated except for occasional annular thickenings met with in section; the enlargement of the xylem parenchyma in this region suggests that they have expanded into the resulting space. Tracheal elements which develop later are more persistent and often show only slight tylose-like invagination of surrounding parenchyma cells between the turns of the helical thickenings. The degree of development of this protoxylem region varies considerably. *Hedychium elatum* showed an extreme type where the vascular region adaxial to the large metaxylem element occupied about one-third of the total section of the bundle. Around the large metaxylem element, the parenchyma cells exhibit a very regular concentric arrangement. Below this dominant element, and separated from it by a layer of parenchyma, is a group of small tracheal elements, mostly angular in section. These elements, which are the last to differentiate, are termed 'commissural connectives' by Skutch (1927) in *Musa*, since the xylem of transverse bundles connects with them. The term 'late metaxylem' is preferred as a less cumbersome expression.

A single layer of conjunctive parenchyma separates the xylem from the abaxial phloem group which, together with the surrounding bundle sheath, is often much wider than the part of the bundle containing the xylem. The phloem consists of sieve-tube elements, companion cells and parenchyma.

The phloem of *Hornstedtia scyphifera* is noteworthy because thick-walled lignified elements are developed forming an irregular network (Fig. 4i). In longitudinal section they are seen to be elongated cells with transverse or slightly oblique end walls and so appear to be sclerosed phloem parenchyma cells. This sclerification, which is more or less confined to the leaf, may be diagnostic for the genus *Hornstedtia* since it was found, much less conspicuously, in *Hornstedtia conica* and is reported by S. & M. for *Donacodes pininga* Bl. = *Hornstedtia* sp. sec. K. Sch.

The bundle sheath is generally separated into an upper and a lower fibre cap by the presence of parenchyma in the median part of the bundle at about the level of the late metaxylem elements. These lateral parenchyma cells are colourless and frequently contain starch grains (Fig. 4a, *k*), occasionally calcium oxalate crystals or silica. On the other hand, the bundle sheath may consist entirely of a continuous layer of fibres, e.g. in *Geostachys taipingensis* and *Hornstedtia* spp. The thickness of the walls of the cells of the upper and lower cap varies with the species. In most species the walls are thick and the lumen is small and the elements are typical fibres, in some, notably *Kaempferia* spp., the

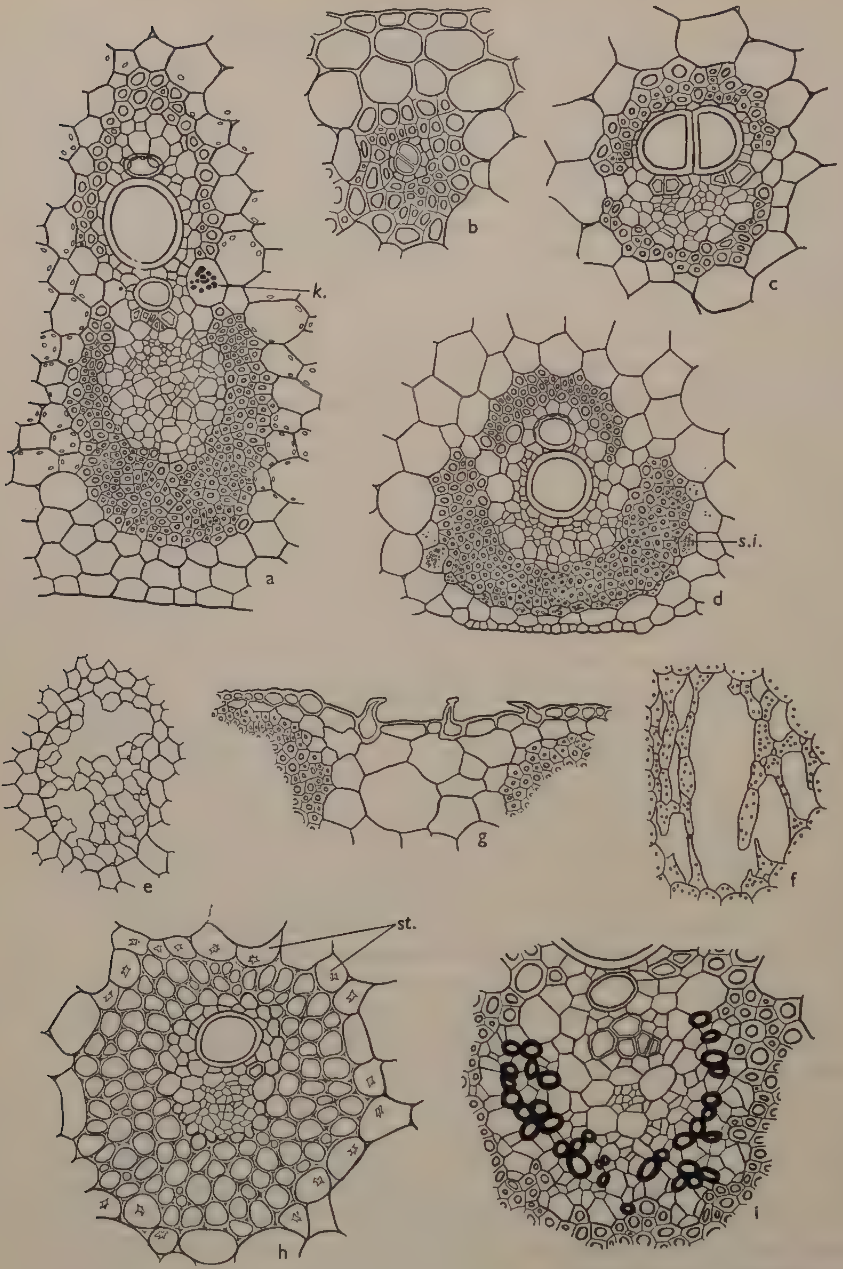


Fig. 4. All from transverse sections. (a) *Alpinia speciosa*, petiole, bundle of main arc, I (× 153). (b) *A. speciosa*, petiole, bundle of upper arc, IV (× 153). (c) *A. speciosa*, petiole, bundle of centre arc, III (× 153). (d) *A. speciosa*, basal part of sheath, bundle of lower arc, II (× 153). (e) *Curcuma* sp., air-canal (partly expanded) from upper part of sheath (× 62). (f) *Curcuma* sp., air canal (fully expanded) from upper part of sheath (× 62). (g) *Alpinia speciosa*, sheath, intercostal region (× 153). (h) *Costus malortieanus*, petiole, bundle of subsidiary (lower) arc showing well-developed collenchyma of the bundle sheath (× 153). (i) *Hornstedtia conica*, midrib, phloem of a bundle of the main arc, I (× 270). *k.*, starch; *s.i.*, silica inclusion; *st.*, stegmata.

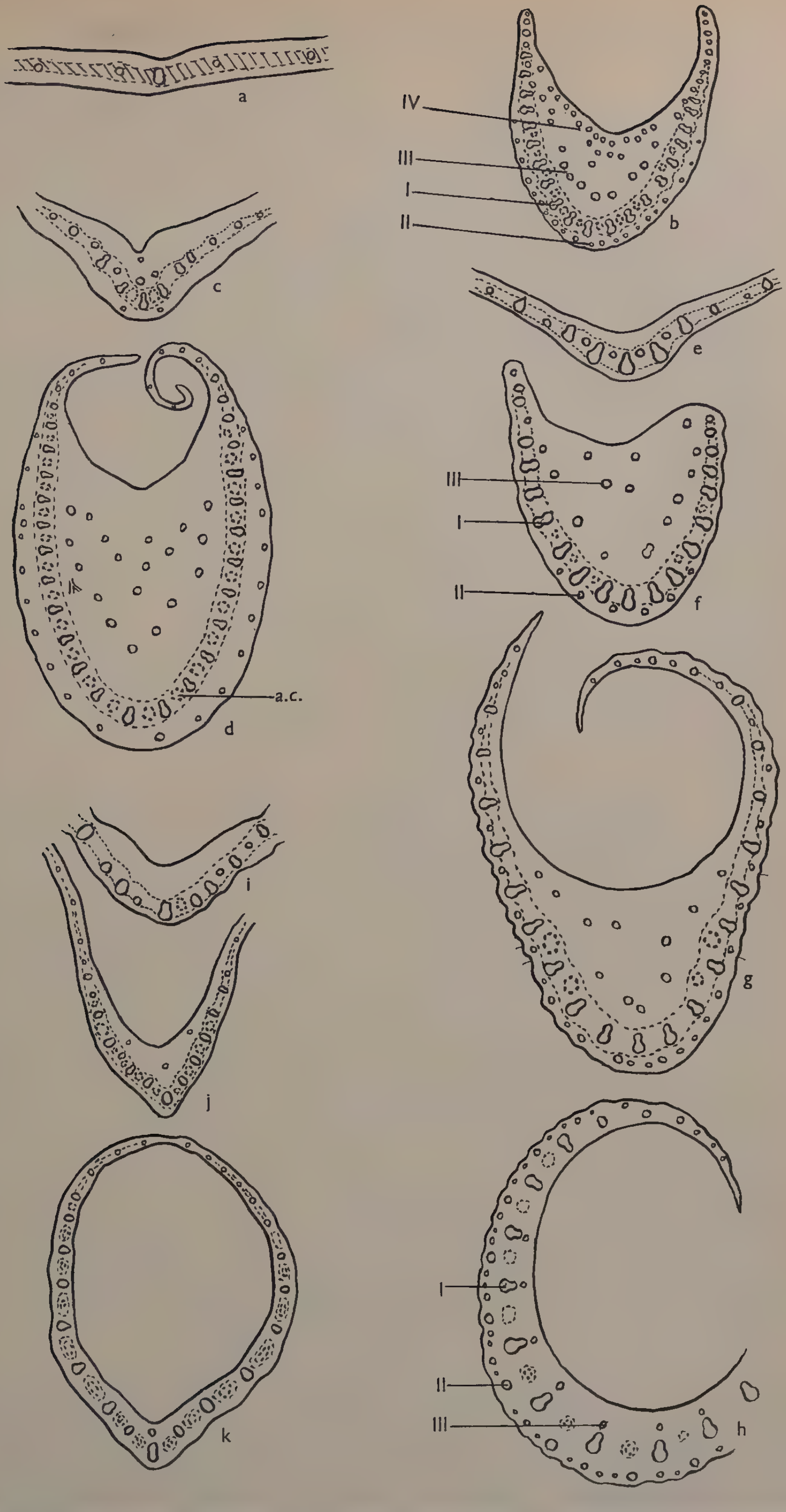


Fig. 5. All from transverse sections. (a) *Burbidgea schizocheila*, midrib region of lamina (×13)· (b) *Hedychium elatum*, petiole (×7). (c) *Kaempferia rotunda*, midrib region of lamina. (d) *K. rotunda*, petiole (×7). (e) *Elettaria cardamomum*, midrib region of lamina. (f) *E. cardamomum*, petiole. (g) *E. cardamomum*, upper part of sheath. (h) *E. cardamomum*, basal part of sheath (×13). (i) *Roscoea humeana*, midrib region of lamina. (j) *R. purpurea*, petiole. (k) *R. purpurea*, upper part of sheath (×7). *a.c.*, air-canal; I, II, III and IV, bundle arcs.

walls are thin and the cells in transverse section are scarcely distinguishable from those of the surrounding ground parenchyma cells, whilst in longitudinal view the elements are evidently prosenchymatous. A general tendency is for the fibres of the adaxial cap to be larger and thinner-walled than those of the abaxial cap. The general structure of the main arc bundles may be modified if the section includes a bundle which is giving off a lateral.

In *Scaphochlamys* and *Roscoea* the bundles are somewhat wider than that described and have several large metaxylem elements instead of the usual one, features which appear to be characteristic for these genera. Laterally the bundles of the main arc of the midrib show a gradual transition in structure to those of the lamina.

The small bundles forming the subsidiary arcs generally have only a single tracheal element and only very rarely is there any extended protoxylem. Xylem parenchyma is little developed or absent. A small phloem group completes the vascular tissues. The bundle sheath consists of a complete ring of fibres and is best developed in the abaxial arc (arc II). The bundles of the adaxial arc (arc III) are often obliquely or inversely orientated. Transverse anastomoses between bundles of the same or different arcs are met with, and often the course of these anastomosing bundles is very irregular.

A characteristic feature of the midrib in this family is a band of assimilating tissue continuous laterally with that of the lamina, e.g. Fig. 6a. This lies at the same level as the main arc bundles which are consequently more or less surrounded by chlorenchyma tissue. In the median part of the midrib region, within the chlorenchyma band and alternating with the main arc bundles, small air canals are often to be found. Since the assimilating tissue and air canals are continuous longitudinally with those of the petiole and sheath, where they are much more conspicuous, their detailed structure is described later (p. 566).

Costoideae

The anatomy of the leaf of *Costus* is so distinct as to merit separate description. In surface view the shape of the epidermal cells and their arrangement in longitudinal files is less regular than is general for the rest of the family. The shape of the subsidiary cells of the stomatal apparatus is also less regular (Fig. 2e). In section the most characteristic feature is the well-developed hypodermis; the epidermis, by contrast, is very narrow (Fig. 3a–c). Generally there is more than one hypodermal layer below each surface, e.g. in *Costus malortieanus*, 2-layered adaxially, 2 to 3-layered abaxially (Fig. 3c). When there is only one layer below each surface (*C. afer* (Fig. 3a)), the hypodermal cells are very large. As a consequence of the well-developed hypodermis the proportion of assimilating tissue to the total lamina width is very small and may be as little as one-fifth (Fig. 3c). The bundle sheaths in *Costus* never extend to the epidermis (Fig. 3b), and this is associated with the absence of any modification of the epidermis cells above the veins.

Only *Scaphochlamys* of the Zingiberoideae approaches this type of lamina structure and shares many of the features of *Costus*.

The midrib region of *Costus* at the standard level studied has a characteristic appearance (Fig. 7a, e). The region is not markedly thickened and may even be constricted. The main arc consists of one to three bundles which approach the adaxial surface, and this is generally accompanied by a single small, abaxial, median bundle. Air canals are absent at this level.

ANATOMY OF THE PETIOLE AND SHEATH

The lamina, although often separated from the sheath by a distinct petiole, which may be long or short, is sometimes sessile. When sessile, sheath and lamina are gradually confluent, with a ligule at the junction of the two regions. The sheaths are long and open on the adaxial side, the margins overwrapping. The succession of enveloping sheaths forms a conspicuous pseudo-stem. The rather different morphology of *Costus* has already been described. Where a petiole was present a standard level just below the lamina insertion was selected for anatomical study. Where the lamina was sessile on the sheath a more arbitrary level at the base of the lamina was chosen. The sheath structure was studied in sections from just below the sheath insertion and at a less precise level towards the base of the sheath.

Zingiberoideae

Epidermis. The epidermis of the petiole shows a structure similar to that of the midrib of the lamina. Stomata are not infrequent, but they are least common or absent on the adaxial surface. In *Aframomum* sp., *Burbidgea schizocheila* and *Catimbium speciosum*, the adaxial epidermal cells in the median part of the section were anticlinally extended, densely protoplasmic and resembled an epithelium. This may be due to a late retention of a meristematic condition. In the sheath there are marked differences between the adaxial (inner) and the abaxial (outer) epidermis. The cells of the adaxial surface are larger, thinner-walled and transversely stretched, this transverse stretching being reflected in the subjacent ground parenchyma cells, notably in *Geostachys taipingensis* where the hypodermal cells are collapsed and much flattened. The adaxial epidermal cells are never papillate; stomata and oil cells are infrequent; hairs are absent. The abaxial epidermis resembles that of the petiole and midrib, and here the ribbing above the veins is often conspicuous, e.g. in *Alpinia* spp., *Burbidgea*, *Catimbium* (Fig. 6e), *Elettaria* (Fig. 5h), *Geostachys*, *Hornstedtia*. In consequence there is a marked contrast between the intercostal epidermal cells and those above the veins (Fig. 4g), and this is slightly apparent even where ribbing is not developed. The epidermal cells within the furrows are larger, more papillate, thinner-walled and often slightly transversely stretched. Hairs, stomata and, to a lesser extent, epidermal oil cells are confined to these furrows. The epidermal cells above the veins have small lumina, and thick walls. Whilst the adaxial epidermis of each successive sheath is closely pressed against the abaxial surface of the next, the ribbing of the abaxial surface and the restriction of stomata to the furrows between these ribs produces a longitudinal aerating system. Although hairs are generally adpressed to the surface because successive sheaths fit so closely together, they are able to protrude some little way above the epidermal surface when they arise within a furrow (Fig. 4g). Towards the base of the sheath stomata are less frequent.

Ground tissue. In the parenchymatous ground tissue of the petiole and sheath the smallest cells are in the subepidermal layers, and there is a gradual transition to the larger, central cells which are associated with conspicuous intercellular spaces. The parenchyma cells on the adaxial side of the petiole, like those in the midrib, may become enlarged. The sclerized subepidermal ground parenchyma cells described for the midribs of *Alpinia javanica* and *Hornstedtia conica* occur also in the petiole and sheath, but are confined to the adaxial side in the sheath and become still less frequent at lower levels. At the base of the sheath in *H. conica* they were represented by a single layer of cells in the median part. Frequently in the wings of the sheath the ground parenchyma cells beneath the epidermis are arranged in layers simulating a hypodermis (*Globba*, *Roscoea*), and this, taken together with the assimilating tissue, gives a section similar to that of the lamina. This is most marked in species of *Costus* (p. 568).

Distribution of bundles. The bundles of the petiole and sheath are arranged in several arcs which are here numbered for convenience I–IV (Figs. 5b, e–h, 6f–i). I is the main bundle arc close to the abaxial surface, and its bundles are all of the same size in the median region, gradually becoming smaller towards the margin. On the abaxial side of arc I there may be an arc of much smaller bundles (II) often made up of alternating larger and smaller bundles, the largest alternating with the bundles of arc I. Adaxial to arc I, in the petiole at least, there are many bundles which have been treated as two groups, although there is often a complete transition in bundle size and position between the two systems. The central system, arc III, consists of intermediate sized bundles arranged irregularly. From this may be distinguished arc IV, a plexus of small bundles

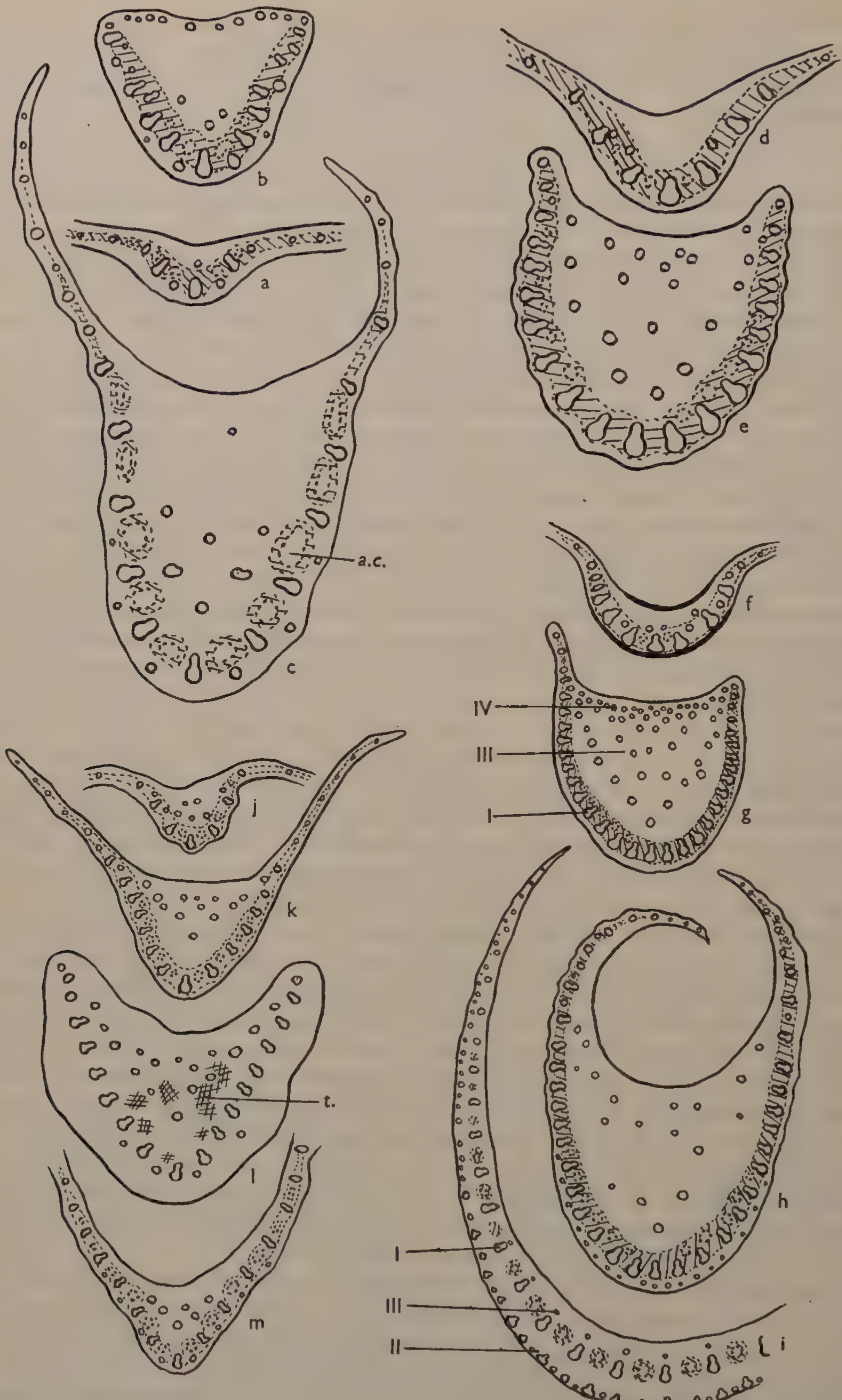


Fig. 6. All from transverse sections. (a) *Globba winniti*, midrib region of lamina. (b) *G. winniti*, petiole. (c) *G. winniti*, upper part of sheath (× 13). (d) *Catimbium latilabre*, midrib region of lamina. (e) *C. latilabre*, petiole (× 13). (f) *Alpinia javanica*, midrib region of lamina. (g) *A. speciosa*, petiole. (h) *A. speciosa*, upper part of sheath. (i) *A. speciosa*, lower part of sheath (× 13). (j) *Zingiber officinale*, midrib region of lamina. (k) *Z. officinale*, basal part of midrib. (l) *Z. officinale*, 'pulvinus'. (m) *Z. officinale*, upper part of sheath (× 7). *a.c.*, air-canal; *t.*, tannin deposits; assimilating tissue cross-hatched in a–i. I, II, III and IV, bundle arcs.

close beneath the adaxial epidermis, e.g. in *Alpinia* (Fig. 6g), *Globba* (Fig. 6b) and *Hedychium* (Fig. 5b).

The degree of development of these bundle arcs varies with the level of section and the species. Arc IV, when present, shows its maximum development in the petiole and is absent from the midrib and the lower part of the sheath. The termination of system IV is marked by gradual fusion with bundles of arc III and accounts for the difficulty in distinguishing the two systems. In several species arc IV is not present, e.g. in *Roscoea* spp. (Fig. 5i, j). S. & M. do not treat the adaxial bundle arc as if it consists of two systems, and it must be admitted that the distinction between the two is never great. Futterer, however, was able to distinguish them in certain species, e.g. in *Brachychilum horsfieldii*.

Arc III, which is not well represented in the midrib, also has its maximum development in the petiole, and diminishes gradually towards the base of the sheath. Here its bundles are generally arranged singly, each immediately adaxial to a bundle of the main arc, with which it finally fuses (Figs. 5h, 6i). Arc II shows increased development towards the base of the sheath. It was infrequently visible in sections of the midrib at the standard level, e.g. in *Brachychilum*, *Curcuma*, *Hedychium*, *Kaempferia rotunda* (Fig. 5c) and it was absent from the petiole of some species, e.g. in *Alpinia* spp. (Fig. 6g), *Catimbium* (Fig. 6e), but became progressively more definite towards the level of the sheath insertion. At the base of the sheath up to three systems of bundles could be distinguished in arc II by their size, the largest alternating in position with the bundles of the main arc within, e.g. in *Elettaria cardamomum* (Fig. 5h). *Roscoea* differs markedly from other members of the Zingiberoideae because arc II is absent at all levels (Fig. 5i–k).

In the wings of the sheath only arcs I and II are present, where they frequently appear as a single arc of alternating large and small bundles.

Comparison of these results with those quoted by S. & M. indicates great constancy in the degree of development of the different bundle systems, which therefore provide useful diagnostic characters. The arrangement of the bundles, as seen in section, at a particular level, often appears characteristic for the genus, as in *Alpinia*, *Catimbium*, *Hedychium*, *Globba*, *Roscoea*, *Kaempferia* and *Scaphochlamys*.

Structure of the bundles. The structure of the bundles is comparable to that described for the midrib. Arc I bundles are precisely similar to the portions of the same bundles in the midrib (Fig. 4a). Each bundle of arc II, especially in the basal part of the leaf sheath, shows a well-developed fibrous sheath which is widest next to the phloem group (Fig. 4d). The abaxial part of the bundle sheath is either continuous with the adaxial part, or is interrupted in a median position by parenchyma cells. One (or rarely more) xylem element is present; extended protoxylem is infrequent. Each bundle of arc III also has a continuous or sometimes interrupted fibre sheath which, however, is not so strongly developed as are the bundle sheaths of arc II (Fig. 4c). A single large tracheal element and several smaller elements are present, but collapse of the first-formed xylem elements is rare. The bundles of the most adaxial arc (IV) are characterized by reduced vascular tissue and a well-developed mechanical sheath (Fig. 4b). Frequently the vascular tissue of these two uppermost arcs is inversely or obliquely orientated, a point previously only recorded for *Donacodes pininga* by S. & M. (*loc. cit.* p. 36).

Bundles may end blindly or fuse one with another. In the former instance, towards the end of the bundle, the vascular tissues are eliminated and the bundle is represented for some distance by a strand of fibres which themselves finally disappear. This can be seen most easily in arc II, which disappears towards the apex of the leaf. Here the bundles are frequently represented by a fibre strand which is reduced to a single file just below where it finally ends. Where bundle fusion takes place, as for example between the remains of arc III and the main arc in the base of the leaf sheath, the vascular tissues of the arc III bundles are eliminated just before fusion and the surviving fibres link on to the adaxial fibre cap of the main arc bundle. There is, therefore, no direct continuity of vascular tissue, and the fact that these systems are independent is particularly noteworthy. There is, however, indirect continuity since these longitudinal systems have their vascular tissues linked by occasional transverse bundles.

A comparison of these results with the descriptions of the development in other Monocotyledons, e.g. Scott & Priestley (1925) for *Tradescantia*, Sharman (1942) for *Zea*, allows some interpretation of these bundle structures and arrangements, although I myself did not undertake any original developmental studies of the Zingiberaceae. The large bundles which form the main arc evidently develop early and basifugally, their protoxylem maturing while longitudinal extension is still in progress. The bundles in arcs II–IV differentiate late and probably basipetally, and their xylem is not generally matured until after extension growth has ceased. Consequently they rarely contain disrupted protoxylem. In the lamina the longitudinal veins of the first order differentiate mainly basifugally, late differentiation of the smaller bundles of the second and subsequent orders takes place basipetally.

Assimilating tissue and air canals. At the same level as, and often surrounding, the main arc bundles is a band of chlorenchyma. Within the band, and alternating with the main arc bundles, is a system of air canals. These extend from the base of the sheath to some level in the midrib of the lamina. These canals are very well developed in *Kaempferia* spp. (Fig. 5d, *a.c.*); they are scarcely recognizable in *Hornstedtia conica* except at the base of the leaf sheath. Whilst the cells of the chlorenchyma band differ from normal parenchyma cells only in containing chloroplasts, those lining the air canals resemble mesophyll cells in their round shape and in their tendency to form short arms enclosing large intercellular spaces. There are all transitions from the structure just described to that of *Hornstedtia* which, in the position occupied by definite air canals in other species, has only a loose tissue of rounded chlorenchyma cells.

The air canals, notably in *Kaempferia*, are interrupted at intervals by transverse vascular bundles embedded in compact chlorenchyma tissue forming partitions or diaphragms. These are visible externally as transverse green bands. Diaphragms which are devoid of vascular tissue also occur, being most distinct in *Curcuma*. Here more or less complete, transverse plates of armed parenchyma cells occur at intervals along the cavities. Continuity through the plates is maintained by the large intercellular spaces. These diaphragms, in which vascular tissues are absent, develop from a single layer of rounded cells (Fig. 4e) which do not multiply by dividing but are partially separated one from another by enlargement of the air canal. At the same time the cells become so drawn out that they maintain contact only at the ends of the extended arms (Fig. 4f). This tissue is comparable to the stellate pith parenchyma which occurs in certain species of *Juncus* and other plants. In other species of the present family, ill-defined transverse diaphragms tend to be formed merely by the extension of irregular long-armed chlorenchyma cells across the cavity.

The air canals communicate with the atmosphere via the stomata in the longitudinal furrows of the sheath. The chlorenchyma band and air space system shows a maximum development in the petiole and upper part of the sheath. Towards the sheath insertion, on the other hand, there is a progressive decrease, the air canals become narrow and the chlorenchyma, now limited to a few cell layers around the canals, is no longer in contact with the bundles of the main arc. The canals and chlorenchyma disappear in the region of the leaf insertion, but the remnants may be recognized in the stem as a loose-celled region in the cortex where starch grains are often abundant.

Costoideae

The anatomy of the petiole and sheath of *Costus* shows so many distinctive characters that it merits a separate description. In the petiole the bundles of arc I are not far below the adaxial surface, and the subsidiary arcs are all abaxial to it (Fig. 7b, f). Futterer, however, reports a weak bundle arc adaxial to the main arc in *C. malortieanus*, but its

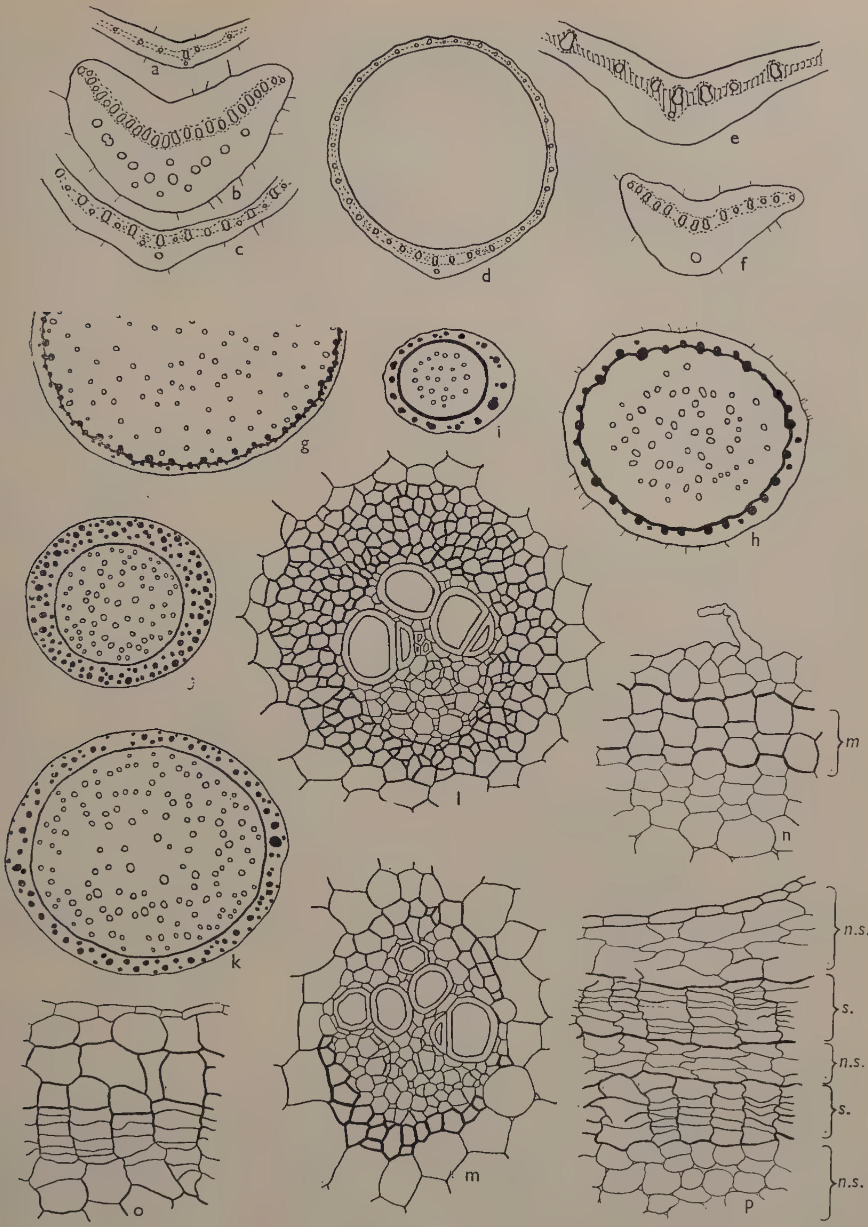


Fig. 7. All from transverse sections. (a) *Costus malortieanus*, midrib region of lamina. (b) *C. malortieanus*, petiole. (c) *C. malortieanus*, median sector of sheath (× 5). (d) *C. rumphianus*, sheath (× 5). (e) *C. afer*, midrib of lamina (× 10). (f) *C. lucanusianus*, petiole (× 10). (g) *C. lucanusianus*, lower part of aerial stem (× 5). (h) *C. malortieanus*, upper part of aerial stem (× 5). (i) *Camptandra ovata*, aerial stem (× 5). (j) *Alpinia sanderae*, aerial stem (× 5). (k) *Hedychium gardnerianum*, aerial stem (× 5). (l) *Alpinia speciosa*, aerial stem, cortical bundle (× 153). (m) *A. speciosa*, aerial stem, bundle from central cylinder (× 153). (n) *Brachychilum horsfieldii*, root, surface layers of cells, *m*, 'metakutis' (× 86). (o) *B. horsfieldii*, rhizome, surface layers of cells, periderm (× 86). (p) *Kaempferia angustifolia*, rhizome, periderm, *s.*, suberized, *n.s.*, non-suberized, cells (× 86). Assimilating tissue cross-hatched in (e).

presence could not be confirmed in the present study. The abaxial subsidiary arc may consist of a single bundle (*C. lucanusianus* (Fig. 7f)), or of several bundles arranged irregularly in up to three arcs, e.g. *C. malortieanus* (Fig. 7b), *C. rumphianus*.

The most striking feature of the section of the petiole of *Costus* is that the fibres of the bundle sheath which are found in the rest of the family are here replaced by collenchyma. This collenchyma sheath forms a continuous, well-developed layer, up to five cells deep, around all the bundles and gives them a characteristic appearance (Fig. 4h). The subepidermal ground tissue of the petiole may also be collenchymatous, as in *C. lucanusianus* and *C. rumphianus*, and at the petiole margin the collenchyma of the ground tissue and of the bundle sheaths is then continuous.

The vascular tissues themselves resemble those in other genera of the family. Those of the bundles of the main arc are arranged as in the main arc bundles of the Zingiberoideae, and similarly the vascular tissues of the subsidiary arc bundles correspond to those seen in the rest of the family. Another similarity is the band of assimilating tissue which surrounds the main arc bundles, but this is much closer to the adaxial surface than it is in other genera. Air canals are absent in the petiole of *Costus*, the bundles being set very close together (Fig. 7b).

The sheath structure of *Costus* is very uniform and characteristic. There is a continuous cylinder of more or less alternating large and small bundles (Fig. 7c) which probably correspond to the basifugal and basipetal systems respectively. Abaxial to the median bundle of this cylinder is a single small bundle which is all that remains of the lower subsidiary arcs of the petiole. Collenchyma, although so characteristic of the petiole, is absent in the sheath, and the cells of the bundle sheath are only slightly thick-walled. A cylinder of assimilating tissue is developed in association with the bundle arc, but air canals appear only towards the base of the sheath and are then never very wide. A peculiarity of the sheath in this genus is that the ground parenchyma develops such large cells that it resembles a hypodermis. This tissue, together with the chlorenchyma band and the single row of bundles, makes the section of the sheath, which is very uniform in width, much like that of the lamina. The similarity is made even more marked, because in any one species the number and relative sizes of the hypodermal layers in the lamina exactly correspond with those that are present throughout the greater part of the transverse section of the sheath. In *C. malortieanus*, for example, the hypodermis of both lamina and sheath is 2-layered adaxially, 2- to 3-layered abaxially.

Petiole of *Zingiber officinale*

The petiole in the available material of *Z. officinale* (grown at Kew) showed several anomalous features which resemble *Costus*. Macroscopically the petiole is colourless and swollen, and has the appearance of a pulvinus. A section of the base of the midrib, just above this 'pulvinar' region, shows a typical structure with two bundle arcs, air canals and chlorenchyma (Fig. 6k). Within the 'pulvinus', however, air canals and assimilating tissue are absent, there is extensive hypertrophy of the ground parenchyma cells and abundant deposition of tanniniferous substances (Fig. 6l, *t.*). The most striking feature is the collenchymatous thickening of the cells of the bundle sheath, which recalls that in the petiole of *Costus*. Below this 'pulvinus' in the upper part of the sheath the structure is again normal (Fig. 6m).

Tropical material of the aerial parts of this species was not available to determine whether these anomalies are confined to the plants grown at Kew. Futterer's description of the petiole of *Zingiber officinale* suggests that the structure described above is not normal.

Anatomy of the aerial stem

Although the aerial stems in the Zingiberaceae may achieve heights of several metres, this is largely due to the development of a pseudo-stem made up of overlapping, closely adpressed leaf sheaths. The true stem (or inflorescence axis) is developed within this structure to varying degrees. *Costus* shows the maximum development of the true stem; this with the short, enveloping sheaths often straggles for some distance. In other species, e.g. *Curcuma* and *Kaempferia* spp., the internodes are not elongated and the sheaths are closely inserted on the short conical stem at the end of the rhizome. In section the stem is circular, or slightly oval near the insertion of the crescent-shaped sheaths.

(1) *The Internode*

Zingiberoideae

Epidermis. In general the epidermis resembles that of the basal part of the sheath, the resemblance being closest near the sheath insertion. As the distance from the insertion is increased, ribbing becomes less conspicuous, stomata and hairs, when present, become very infrequent.

Fibrous cylinder. A feature of the stems of this family is the cylinder of fibre-like cells separating a cortex from the central cylinder (Fig. 7g–k). It consists of a continuous layer, 3–4 cells deep, the cells being identical in appearance with the fibres of the bundle sheath. There is, however, a transition from ground parenchyma cells to the thick-walled fibres by way of thin-walled prosenchymatous elements. When relatively undifferentiated this region consists of parenchyma or prosenchyma files, and, when more strongly differentiated, cell divisions are reduced and the cells have fibre-like forms with a corresponding increase in thickness of the cell wall.

Early workers spoke of this layer as the 'inner sheath', but the term fibrous cylinder is used here to prevent possible confusion with the leaf sheath. The layer is continuous, except at the nodes where it is interrupted by the entry of leaf traces. Here also the bundle sheaths of the traces become confluent with the tissues of the fibrous cylinder for a short distance.

Occasionally the fibrous cylinder is absent, e.g. in *Globba* spp. and *Scaphochlamys breviscapa.*

Cortex. The relative widths of the cortex and central cylinder separated by the fibrous cylinder, are very variable. The cortex is rarely very narrow, generally about one-quarter to one-fifth of the width of the central cylinder (Fig. 7i, j), and it may be up to one-quarter of the total diameter of the stem, as in *Roscoea purpurea.* The assimilating tissue and air canals of the sheath may cease abruptly at the insertion, e.g. in *Alpinia speciosa*, or persist for some distance below the node into the cortex, e.g. in *Cautleya spicata* and *Scaphochlamys breviscapa.* The termination of the assimilating tissue is often represented in the cortex of the stem by a cylinder of rounded cells with occasional chloroplasts or starch grains and associated with large intercellular spaces. Occasionally a slight collenchymatous thickening of the subepidermal ground parenchyma cells is observed (*Alpinia* spp., *Camptandra ovata*). Sometimes, also, the parenchyma adjacent to the bundles and the fibrous cylinder is collenchymatous (*Roscoea humeana*). A more conspicuous development of collenchyma may occur at the junction of sheath and stem (*Alpinia speciosa*).

A characteristic feature of the Scitamineae is the presence of a system of bundles which is confined to the cortex. In the Zingiberaceae it may form a single ring of bundles (*Camptandra ovata* (Fig. 7i)), but generally the bundles are arranged in about three to four irregular rings (Fig. 7j, k). Comparison of my results with those of S. & M. suggest that the number of rings is constant for a given species at a particular level, although it is often impossible to determine the numbers exactly. This bundle system is quite distinct from, and is often separated some distance from, the fibrous cylinder (Fig. 7i–k), although frequently the outermost bundles abut on the epidermis (*Aframomum* sp., *Cautleya spicata*, *Hedychium coccineum*).

The individual bundles resemble, in their anatomy, the bundles of the outermost arc (II) of the sheath, of which they are a downward continuation. They are circular in section with a well-developed, complete fibre sheath. This may be up to 8 cells deep as in *Alpinia speciosa* (Fig. 7l). The bundle sheath is generally widest where it abuts on the xylem and only rarely is it widest external to the phloem (*Brachychilum horsfieldii*). The walls of the individual fibres of the bundle sheaths vary greatly in thickness from species to species, and are thickest in *Hornstedtia conica*. The xylem consists of a single large element or several smaller ones (Fig. 7l), but there is little evidence of extended protoxylem. The xylem is separated from the fibres of the bundle sheath and the small phloem group by parenchyma. Occasionally these cortical bundles show oblique or inverse orientation of their vascular tissues. The size of the bundles varies, and in some species there is an irregular alternation of large and small bundles, the smallest sometimes lack vascular tissues and then appear as a group of fibres. The bundles of arc I are to be seen in sections of the internode as they pass across the cortex to the central cylinder. Transverse anastomoses between cortical bundles may be met with occasionally, but there is no regularity in their distribution.

Central cylinder. The central cylinder contains numerous bundles scattered irregularly in a uniform ground parenchyma. The most striking difference in the structure of these bundles, compared with those of the cortex, is the weak development of the mechanical tissue of the bundle sheath, which forms an interrupted layer one or two cells deep (Fig. 7m), and often consists of isolated fibres. The rest of the bundle sheath is formed of small-celled parenchyma. The arrangement of the vascular tissue corresponds to that in the cortical bundles, but extended and collapsed protoxylem is much more frequent.

The region of transition between aerial stem and rhizome shows a change in structure. The bundles take up a more irregular, oblique course, the fibrous cylinder disappears and the fibres of the bundle sheaths are replaced by collenchyma. The short stems of *Curcuma* and *Kaempferia*, where no internodal elongation takes place, show a similar structure.

Costoideae

The anatomy of the internode of *Costus* differs in several aspects from that in the remainder of the family (Fig. 7g, h):

(i) The cortex is very narrow, representing only a small fraction of the total diameter of the stem; at its narrowest it may be only two or three cells wide (Fig. 7g).

(ii) The fibrous cylinder has an undulate outline in section whereas, in the rest of the family, it does not show this feature.

(iii) The bundles of the cortical system are embedded in the fibrous cylinder. There is an approximate alternation of two small with one large bundle, the latter being more deeply placed. The fibres of the bundle sheaths and the fibrous cylinder are confluent, except in certain of the innermost and outermost bundles which lie free in the ground parenchyma.

The structure of the bundles and differences between cortical and central cylinder systems, are similar to those in the Zingiberoideae.

These points of difference have been established for all species of *Costus* which have been studied (S. & M.; Smith, 1941), and are evidently characteristic of the genus and probably of the subfamily Costoideae.

(2) *The node*

Zingiberoideae

The appearance of the node in transverse section does not differ markedly from a similar section of the internode in this subfamily. This is because the bundles which enter from the leaf sheath are inserted gradually into the stem. In longitudinal view the bundles deviate only slightly from the vertical and extend for several internodes in the stem before they disappear.

The two arcs of bundles which are found at the base of the leaf sheath remain distinct from each other in the stem. Followed downwards from the sheath into the stem, the bundles of the main arc, I, pass gradually into the central cylinder to which region they become confined. The bundles of the outermost arc, II, do not enter the central cylinder but form the cortical system, which is so characteristic of the stem in transverse section. No fusions take place between bundles of the two different systems.

Costoideae

Unlike the nodal region in members of the Zingiberoideae, the nodes in the aerial stem of *Costus* develop a conspicuous plexus of vascular tissue. This nodal plexus is produced by:

(i) The *horizontal* insertion of many of the bundles from the leaf sheath.

(ii) Frequent and irregular anastomoses between different bundles.

Although the bundles in the leaf sheath of *Costus* are arranged in a single cylinder, they can be classified as large and small bundles which more or less alternate. Only the larger bundles possess protoxylem. These two types of bundle may be compared to the systems of bundles arranged in two arcs in the Zingiberoideae. It is the larger bundles which are inserted horizontally and pass into the central cylinder to which they become confined. The small bundles, which alternate with the larger bundles in the leaf sheath, form the peripheral system of bundles which are embedded in the fibre cylinder of the stem.

Although the structure of the node and the course of the vascular bundles in the stem has not been worked out in detail for any species of the family, the observations which have been made indicate that there are marked differences between the subfamilies in these respects. Fundamentally, however, both subfamilies are similar in that they have two independent bundle systems, one confined to the central cylinder, the other to the cortex.

It is also noteworthy that the nodal plexus of *Costus* is associated with the presence of axillary buds in the aerial stem. In the Zingiberoideae there is no plexus developed at the node, and axillary buds are absent from the aerial stem.

THE RHIZOME AND ROOT

When the structure of the rhizomes and roots of several species are compared it is found that there are few differences. Consequently, only a brief description of the more conspicuous features is included.

(1) *The rhizome*

In those members of the Zingiberaceae with a well-developed rhizome, this is sympodial, consisting essentially of successive branch insertions. Whilst each segment of the rhizome is morphologically equivalent to the aerial stem, and there is a fundamental similarity in the anatomy of the two organs, functional modifications, such as its development as a storage organ, the reduction of the leaves to scales and the development of lateral roots and axillary buds bring about important changes. Accurate transverse sectioning of the rhizome is often impossible, owing to its irregular shape and the tortuous course of the vascular bundles.

The outer cortical cells of the rhizome are occasionally suberized. Where the suberization is associated with cell division a 'periderm' may be formed and is not infrequent in members of the Zingiberaceae. This periderm is of the storied or *etagen*-type in which cell divisions occur in several successive cell layers, e.g. *Brachychilum horsfieldii* (Fig. 7o). Occasionally, as in *Kaempferia angustifolia* (Fig. 7p), the layers of cells in which division and subsequent suberization takes place (*s.*) may be separated from each other by layers of cortical cells in which no cell division and no suberization occurs (*n.s.*). In many species, however, no periderm tissues are developed, and the outer cortical tissues retain their primary structure. Apparently the development of periderm tissues is associated with habitat conditions since they are not found in all individuals of the same species. Consequently, the presence of periderm is of no diagnostic value.

The rhizome is separated into cortex and central cylinder by an endodermis, which is not present in the aerial stem. The cortex contains numerous scattered vascular bundles. Immediately within the endodermis is a narrow cylinder of vascular tissue, very conspicuous to the naked eye in a transverse cut through the rhizome. In it individual vascular bundles cannot be identified, and the conducting tissues in transverse sections of the rhizome are cut in all planes. The central cylinder itself contains numerous scattered vascular bundles. The structure of the vascular bundles of the cortex and central cylinder resembles that of the bundles in the aerial stem, but mechanical tissues are less well developed.

The diameter of the rhizome varies considerably in different species. The rhizome may be large owing to the development of much parenchyma and the vascular bundles are then isolated, e.g. *Zingiber officinale*. In other species, e.g. *Elettaria cardamomum*, the rhizome is narrow and the vascular bundles are close together. Generally the parenchyma of the ground tissue contains abundant starch.

(2) *The root*

Owing to the great variability in size and age of roots it is not easy to define standard positions from which sections may be taken for comparative purposes. Whenever possible, however, roots of a similar size were examined.

Unlike the rhizome, the formation of a periderm in the outer cortical layers is rare in the root. However, the cells immediately within the piliferous layer are often differentiated from the inner cortical layers in being tightly compacted, arranged in radial rows and possessing suberized walls (Fig. 7n, *m*.). This layer is called the *exodermis* by S. & M., and the *interkutis* by Futterer. It has been termed *metakutis* by later German authors, e.g. Philipp (1923). Within the exodermis there is occasionally a narrow cylinder of fibres, e.g. in *Elettaria cardamomum* (Fig. 8p). The boundary between the cortex and the stele is represented by an endodermis (Fig. 8o). In old roots the endodermal cells show the U-shaped thickenings characteristic of Monocotyledons. Within the endodermis is a conspicuous single-layered pericycle, although according to S. & M. this may sometimes be 2-layered. Much of the tissue of the stele is ground or conjunctive tissue in which the conducting elements are embedded. The cells of the ground tissue are fibre-like, with thickened, unlignified walls. At the centre of the stele, in most of the roots examined, is a conspicuous pith-like tissue consisting of large, thin-walled, rounded parenchyma cells.

The roots are polyarch; the protoxylem at the poles of the xylem arms generally abuts on to the pericycle. The phloem groups, which alternate with the xylem arms, generally have a limited radial extent (Fig. 8o). Occasionally, however, they are considerably extended radially towards the centre of the root, as in *Brachychilum horsfieldii* and *Hedychium gardnerianum*. Sometimes isolated phloem groups are found within a short distance of the pith, a condition frequent in *Hedychium* species.

HAIRS

(1) *Types of hair*

Zingiberoideae

Superficially the Zingiberaceae show little pubescence, and anatomical study reveals only a few types of trichomes with limited distribution. Some of these hairs are not visible macroscopically. Although the range of structure is more or less continuous, several types have been established by Staudermann (1924) and are described separately below.

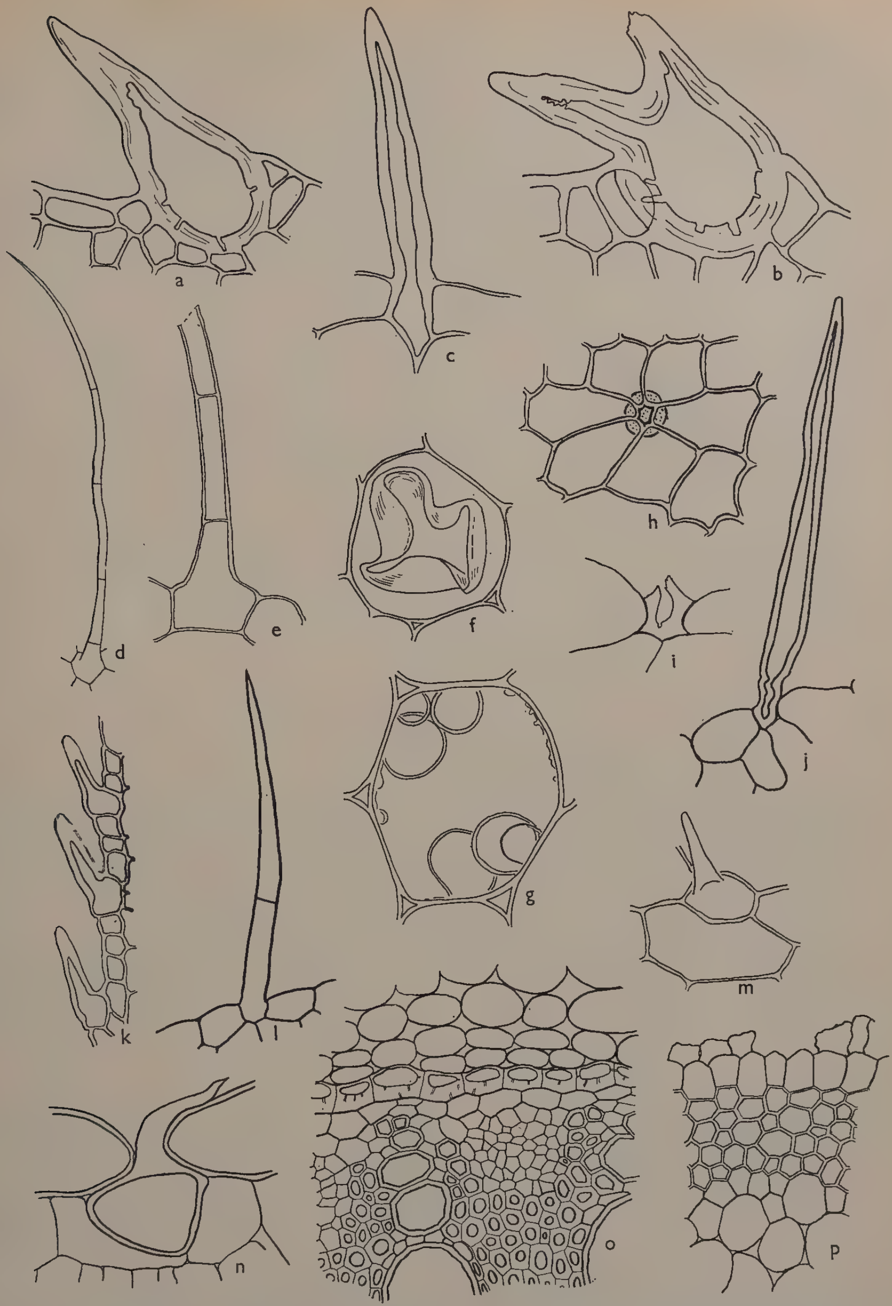


Fig. 8. (a) *Aframomum* sp., hair from margin of leaf (× 210). (b) *Aframomum* sp., 2-pointed hair from margin of leaf (× 383). (c) *Elettaria cardamomum*, t.s. midrib region of lamina, hair from abaxial surface (× 383). (d) *Costus malortieanus*, lower epidermis of lamina, multicellular hair (× 95). (e) *C. malortieanus*, t.s. lower part of sheath, basal part of a multicellular hair (× 383). (f) *Alpinia speciosa*, t.s. petiole, tannin cell from ground parenchyma (× 417). (g) *A. speciosa*, t.s. basal part of sheath, tannin cell from ground parenchyma (× 417). (h) *Zingiber officinale*, lower epidermis of lamina, hair base in surface view (× 270). (i) *Z. officinale*, t.s. petiole, base of detached hair (× 383). (j) *Z. officinale*, t.s. petiole, attached hair (× 270). (k) *Globba bulbifera*, hairs on margin of leaf (× 153). (l) *Curcuma* sp., t.s. rhizome, 2-celled hair (× 270). (m) *Costus lucanusianus*, lower epidermis of lamina in surface view, unicellular hair (× 383). (n) *Hornstedtia conica*, t.s. lamina, sunken hair in adaxial surface (× 383). (o) *Elettaria cardamomum*, t.s. root, endodermal region (× 270). (p) *E. cardamomum*, t.s. root, outer cortical layers (× 153).

(i) The first type corresponds to his '*Stacheln*' (prickles), defined as one- or more-celled hairs with strongly thickened walls and a massive apex which is never more than twice as long as the basal diameter. Hairs of this type were found only in *Aframomum* sp. (Fig. 8a), and were confined to the leaf margin. They are unicellular with thick lamellate walls and with conspicuous pits in the wall of the massive base, which is often partly overarched by the surrounding epidermal cells. The short point is often branched (Fig. 8b). These hairs are irregularly distributed at the leaf margin, often two to three are grouped together. Somewhat similar hairs occur in several other species, notably in the leaf sheath of *Hornstedtia conica* and the leaf margin of *Alpinia javanica*, *Cautleya spicata* and *Hornstedtia conica*, where the marginal hairs are large, thick-walled and with bulbous bases.

(ii) The most frequent hair type is the '*Borste*' (bristle) of Staudermann. These are defined as one- or more-celled, cylindrical, generally pointed and stout hairs, but with a certain elasticity and a length five to fifteen times the basal diameter. They were found in the following genera: *Aframomum*, *Alpinia*, *Brachychilum*, *Burbidgea*, *Catimbium*, *Cautleya*, *Curcuma*, *Elettaria*, *Elettariopsis*, *Hornstedtia*, *Roscoea* and *Zingiber*. They vary much in size, even on a single plant; the largest were those on the ligule of *Hornstedtia scyphifera* where they are up to 1·5 cm. long. Generally, the largest hairs are those of the leaf margin, where they are also bulbous-based (Fig. 8k) and resemble type (i) described above. In *Hornstedtia* and *Renealmia* spp. the bases of the hairs are very dilated and they are sunken below the epidermal level, a short point projecting above the leaf surface (Fig. 8n). The structure of these hairs again recalls that of type (i). In the other species the hairs are only slightly depressed, and the apex of each hair is long and projecting, e.g. in *Elettaria cardamomum* (Fig. 8c). Hairs of the bristle type are frequently adpressed when they arise on the epidermis of a leaf that is in contact with that of a neighbouring leaf, e.g. in overlapping leaf sheaths (Fig. 4g).

Wall thickness varies considerably, and may be uneven in a single hair. The lumen then has a corresponding uneven outline and may be so completely interrupted as to appear multicellular. Multicellular hairs are, however, absent from the Zingiberoideae, with the exception of occasional two-celled hairs on the stem of *Curcuma* (Fig. 8l). Thick-walled hairs often show pitting in the embedded basal region. Thicker-walled hairs were seen to be lignified in *Alpinia sanderae*, *A. speciosa*, *Catimbium latilabre*, *Elettaria cardamomum*, *Geostachys taipingensis*, *Hornstedtia conica* and *H. scyphifera*. The lignification of hairs may be confined to those of a particular region of the plant, e.g. *Catimbium* (petiole), *Hornstedtia scyphifera* (sheath); or lignified and unlignified hairs may be intermingled (*Alpinia sanderae*). All thick-walled hairs take up safranin, even when tests for lignin with phloroglucinol and HCl give a negative result.

(iii) The third, and least precise type of hair is the 'Weichhaare' (soft or delicate hair) of Staudermann, which he defines, inadequately, as a one- or more-celled, simple, blunt or pointed hair. Staudermann quotes the hairs of *Kaempferia rotunda* as an example of this type, and my description of them refers to the same species. The term 'Weichhaare' includes hairs which differ from the 'Borste' in their greater average length and in having the cell walls most strongly thickened at their bases. The most distinctive feature is that they are easily detached at the slight constriction of wall and lumen at the surface of the leaf (Fig. 8i, j). The persistent base appears to become slightly compressed by turgor expansion of the surrounding epidermal cells, which in surface view may show a radial arrangement around the hair base (Fig. 8h). Generally, only the thickened bases of these hairs take up safranin in permanent preparations.

The best example of this hair type are the hairs of *Scaphochlamys erecta* (Fig. 2c), where the walls of the hair are thin and the hair itself is somewhat contorted. Trichomes that can be interpreted as 'Weichhaare' occur also in *Globba bulbifera*, *Hedychium elatum* and *Zingiber officinale*.

Costoideae

The hairs of *Costus* differ in two important respects from those of the rest of the Zingiberaceae and probably the difference applies to the whole of the subfamily Costoideae.

(i) Whilst the hairs in the Zingiberoideae may be sunken, and often are markedly so, the hairs of *Costus* are always superficial (e.g. Fig. 8e).

(ii) Whereas the hairs of the Zingiberoideae, except for occasional 2-celled trichomes on the short stems of *Curcuma* spp. (Fig. 8l), are always unicellular, the hairs of *Costus* are frequently uniseriate. They may be long and thin-walled, and may be divided by up to five delicate transverse septa, e.g. in *C. malortieanus* (Fig. 8d, e). In *C. lucanusianus*, multicellular hairs are confined to the leaf margin, the adaxial leaf surface in this species bears short unicellular bristles ('Borsten') only (Fig. 8m). That uniseriate hairs are also to be found in other genera of the Costoideae is indicated by Staudermann's record of them in *Tapeinochilos hollrungii*.

The hairs in the family as a whole are generally colourless without special inclusions. They may occasionally contain tannin, since those at the leaf margin often appear yellow in untreated preparations.

Evidently the type of hair offers useful diagnostic features serving to distinguish the two subfamilies Costoideae and Zingiberoideae. Genera also show some uniformity in the type of hair they bear, notably the sunken shortly-pointed hairs of *Renealmia* and *Hornstedtia*. The stellate hairs recorded by S. & M. for *Renealmia exaltata* probably refer to branched hairs of the type seen in *Aframomum* (Fig. 8b).

(2) *Distribution of hairs*

On the lamina, the hairs may be confined to the margin and then they may be present only towards the apex. Where hairs occur also on the surface, the marginal hairs are distinguished by their greater size, bulbous bases and thicker walls (Fig. 8k). Marginal hairs always incline towards the apex. The hairs on the lamina may occupy both surfaces equally (*Alpinia javanica*), or may be more abundant on the adaxial surface (*Elettaria cardamomum*) or the abaxial surface (*Hornstedtia conica*). They may be found on the abaxial surface only (*Cautleya spicata*). There may be differences between the hairs on the two surfaces, the adaxial surface having the largest hairs (*Costus malortieanus*, *Hornstedtia conica*). In *Alpinia javanica*, although the hairs are scattered over the whole surface, they are most frequent near the veins; in *Cautleya spicata* they are restricted to the veins, whilst in *Hornstedtia*, the hairs form two rows on either side of, but never directly above, the veins (Fig. 2d). Surface hairs often incline towards the apex, generally more or less parallel with the veins. Hairs are often well developed and conspicuous on the ligule (*Hornstedtia scyphifera* and *Costus malortieanus*). Where the sheath is ribbed, hairs, when present, are generally confined to the bases of the furrows. Hairs are sometimes found on the stem only near the leaf insertions. Rarely, hairs occur on the rhizome and here again they may be associated with the scale insertions as in *Alpinia speciosa*.

The distribution of hairs in any one species is very irregular. The following patterns were noted: *Brachychilum horsfieldii* (leaf margin, scale leaves and rhizome); *Burbidgea schizocheila* (lower part of sheath only); *Catimbium latilabre* (petiole and lower part of sheath only); *Geostachys taipingensis* (sheath only); *Hedychium malayanum* (rhizome only). *Costus malortieanus* represents an extreme where all parts are covered with numerous hairs. *Camptandra ovata*, species of *Hedychium*, *Kaempferia* and *Roscoea*, are glabrous. Of the species of *Roscoea* which were examined, *R. purpurea* was the only one in which hairs were seen, and even here they were rare.

The presence or absence of hairs may afford a method of distinguishing families within the Scitamineae. Staudermann says that hairs are absent from the Cannaceae and Musaceae and present in the Marantaceae and Zingiberaceae.

Cell inclusions

(1) *Calcium oxalate*

Calcium oxalate crystals were present to some extent in all the plants examined. The crystals were distinguished from the silica inclusions by their marked bi-refringence between the crossed Nicols of the polarizing microscope. Although most of the observations were made on permanent mounts, they were frequently checked on unstained sections, since small crystals tend to be dissolved by the clearing agents used. Although the crystals vary considerably in shape, they are all referable to the rhombohedral system and are rhombohedral, prismatic, tabular, or when one axis is very much elongated, rod-shaped. The crystals vary in size from aggregates of minute bodies forming sand (*Roscoea* spp., *Costus malortieanus*), to single large crystals, one in each cell (*Globba* spp.). A whole range of intermediate types is found, the most frequent being groups of small crystals (Fig. 9v).

The distribution of calcium oxalate crystals suggests that they are associated with carbohydrate synthesis. In the lamina, where they may be very abundant, and in the petiole and sheath, they are mostly confined to the chlorenchyma. At progressively lower levels in the leaf they become more numerous in the ground parenchyma. In the lamina they may also occur in the hypodermis, but only very rarely in the epidermis. They are less abundant in the stem, infrequent in the underground parts, and generally absent from the roots. Exceptions can be found to these generalizations, e.g. in *Brachychilum horsfieldii* crystals are frequent in the root and they are abundant in the rhizome of *Costus rumphianus*.

S. & M. suggest that the presence of large calcium oxalate crystals may be diagnostic of certain species, but they also report that there may be variation in crystal content in different samples of the same species (*Alpinia javanica*). In *Globba* spp. each cell of the abaxial hypodermis of the leaf frequently contains a single large crystal, and this may be characteristic of the whole genus (Fig. 2i). The abundant coarse crystal sand in the leaves of *Roscoea* spp. may also be diagnostic for the genus.

(2) *Silica*

S. & M. devote considerable attention to the nature and distribution of silica bodies in the Zingiberaceae, but indicate that their occurrence and distribution need further investigation. It is hoped that the following account may help to clarify the situation, especially as such features afford valuable systematic data within the family. For the detection of silica, cleared preparations are essential, otherwise the smaller particles are easily missed. The granules are then visible by the light they reflect and are distinguished from calcium oxalate crystals by not being bi-refringent. S. & M. also used incineration techniques to establish the nature of these substances.

Although there is confusion in the terminology applied to these silica inclusions, a subject which is discussed fully later (p. 586), the following term is used throughout this section. The word 'stegma' (pl. 'stegmata') is applied to each more or less isodiametric cell containing a single large silica body, the cells occurring in longitudinal series always adjacent and parallel to the fibres of the bundle sheath. The wall of the stegma adjacent to the fibre may show a U-shaped thickening (Fig. 9r), but this is largely the secondary wall of the fibre itself, although this may be obscure when the middle lamella cannot be distinguished.

Zingiberoideae

The silica bodies in the stegmata of this subfamily are large, spherical bodies with an irregular, granulose surface (Fig. 9p, q). Typical diameter measurements of these bodies are 7 μ in *Alpinia javanica*, 5 μ in *Elettaria cardamomum* and *Geostachys taipingensis*. The rows of stegmata, which may be continuous or interrupted, are almost confined to the

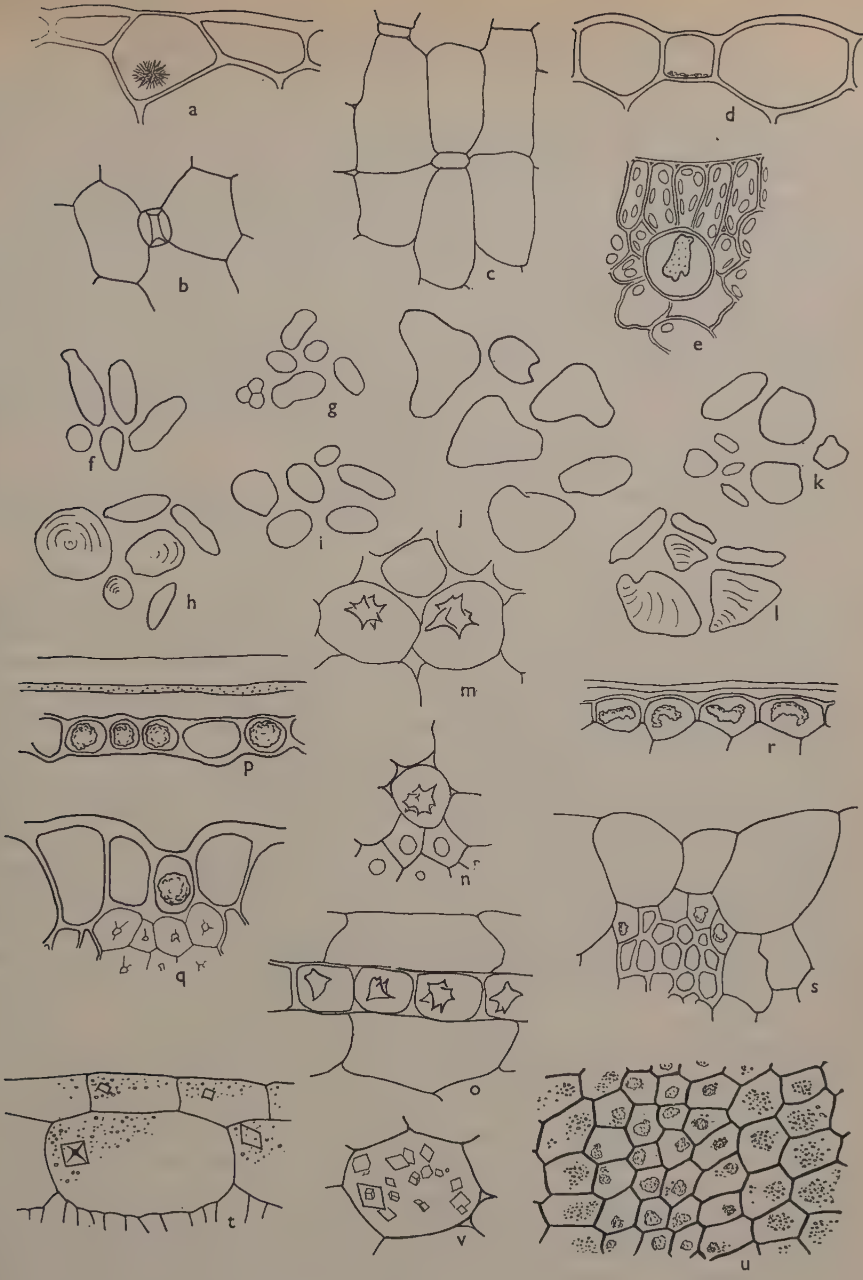


Fig. 9. (a) *Alpinia speciosa*, t.s. petiole, oil cell in epidermis (×477). (b) *Burbidgea schizocheila*, lower epidermis of lamina, oil cell in surface view (×173). (c) *Elettaria cardamomum*, l.s. root, oil cells in the ground parenchyma of the cortex (×153). (d) *Roscoea humeana*, l.s. lamina, oil cell in epidermis (×317). (e) *Hedychium gardnerianum*, l.s. lamina, oil cell at the junction of palisade and spongy-mesophyll (×383). (Oil cell at a slightly higher level of focus than the surrounding cells.) (f-l) Starch grains from the rhizome (×383). (f) *Elettaria cardamomum.* (g) *Alpinia speciosa.* (h) *Kaempferia kirkii.* (i) *K. gilberti.* (j) *Costus lucanusianus.* (k) *Zingiber officinale.* (l) *Hedychium gardnerianum.* (m-o) Stegmata of *Costus.* (m) *C. rumphianus*, t.s. petiole, stegmata adjacent to the collenchyma of the bundle sheath (×417). (n) *C. lucanusianus*, t.s. aerial stem, stegmata adjacent to the fibres of a cortical bundle (×417). (o) *C. lucanusianus*, l.s. aerial stem, stegmata (×317). (p, q) *Alpinia javanica* (×460). (p) l.s. lamina, stegmata from abaxial surface, adjacent to a fibre of a bundle sheath; the lumen of the fibre is shaded. (q) t.s. lamina, stegmata in epidermis, adjacent to the fibres of a bundle sheath. (r, s) *Kaempferia kirkii* (×417). (r) Leaf seen through adaxial surface, stegmata in a hypodermal position, adjacent to the fibres of a bundle sheath. (s) t.s. lamina, hypodermal stegmata. (t) *Geostachys taipingensis*, t.s. lamina, silica inclusions in adaxial epidermis and hypodermis (×317). (u) *Catimbium speciosum*, upper epidermis, silica inclusions (×383). (v) *Hedychium coccineum*, t.s. basal part of sheath, ground parenchyma cell with calcium oxalate crystals (×317).

epidermis of the leaf lamina (Fig. 2a, b), with one wall adjacent to, and parallel with, the fibres of the bundle sheath extension (Fig. 9p, q). Rarely, the stegmata rows are locally separated from the fibres by one (sometimes two) small hypodermal cells. When present, the stegmata occur on both leaf surfaces, but they were restricted to the lower epidermis in *Aframomum* sp. In *Hornstedtia conica* stegmata were found in other cells than those of the epidermis. In the leaf sheath of this species they were situated between the epidermis and the fibres of the bundle sheath.

The stegmata in *Kaempferia kirkii* show several anomalies. This is the only species in the tribe Hedychieae which possesses stegmata (Table 1) and these are always hypodermal in position in the lamina (Fig. 9s), but they also occur, in a deep-seated position, in the petiole and sheath. The shape of the silica bodies in this species is also distinctive, for they are elongated, cylindrical or crescentic (Fig. 9r) and they often show a median constriction or are divided into two distinct bodies.

A second type of silica inclusion consists of a few to many, large to minute, granules. All silica deposits of this type are here referred to as sand, although the appearance of the inclusions is very variable. S. & M. have already indicated that all stages of transition between the large silica bodies of the stegmata to a fine sand can be recognized.

The cells containing transitional types of silica inclusion are sometimes continuous with a row of stegmata. The fact that some of the cells contain a single large body surrounded by others that are smaller suggests that the smaller bodies may be formed when large ones break up (Fig. 9u). This type, consisting of one fairly large and numerous smaller granules in the same cell, may be more widely distributed in certain species. In *Alpinia speciosa* (Fig. 2f) all epidermal cells, other than those above the veins, showed a single large body (diameter 4 μ), together with many minute granules. *Geostachys taipingensis* (Fig. 9t) is similar, but here the silica occurs in the hypodermal cells as well as in the epidermal cells. A peculiarity of the large bodies in these cells of this species is that they are cubical or rhombohedral with a very crystalline appearance, although they are not birefringent. The large bodies of the epidermal cells (diameter 5 μ) are smaller than those of the hypodermal cells (diameter 8–12 μ). A further stage in the transition from single silica bodies to sand is shown in species of *Alpinia* where the cells adjacent to the fibres of the bundle sheath contain several moderate sized granules (Fig. 4d, *s.i.*). Finally true silica sand is found, although the size of the grains is very variable, even within the same cell.

Silica sand may occur in the same cell as calcium oxalate crystals. It is frequent in the leaf and was found in the epidermal cells of *Alpinia bracteata* and *Catimbium speciosum*. In a surface view of the epidermis in the last species one can see a gradual transition from true stegmata overlying the veins to the silica sand in the intercostal regions (Fig. 9u). In all those species with silica inclusions in the intercostal regions of the epidermis (*Alpinia javanica*, *A. bracteata*, *Catimbium speciosum* and *Geostachys taipingensis*), it is noteworthy that the subsidiary cells rarely, and the guard cells never, contain silica (Fig. 2f). This was also noted by S. & M. Silica sand was widely distributed in the mesophyll of *Renealmia* sp., in *Globba bulbifera* the sand in the lamina was confined to the parenchyma of the bundle sheath (Fig. 2i, *s.i.*).

In general, in other parts of the plant, silica sand is associated with the vascular bundles. In the petiole, sheath and stem the sand is usually concentrated in the ground parenchyma cells surrounding the bundles and, in the stem, in the cells adjacent to the fibrous cylinder. This association between silica and vascular tissues is less marked towards the base of the plant, and silica is widely distributed in the rhizome. In the aerial stem silica sand is abundant in the cortex, but the amount decreases in the inner tissues and it may be absent from the central cylinder (*Alpinia javanica*). The granules in the cortical parenchyma are often somewhat larger than those in the parenchyma of the central cylinder. Silica appears to be completely absent from the root.

The type and distribution of silica inclusion are of great diagnostic value in the

Zingiberoideae. Table 1 shows the distribution of silica in this subfamily, a + denoting that it is present, a − that it is absent. The relative quantity is not indicated and a dot has been inserted where a record is not available.

The table shows that stegmata are absent from all species of the tribes Hedychieae and Globbeae so far examined, with the single exception of *Kaempferia kirkii*. Stegmata are present in most, but not all, species of the tribe Alpinieae, some species of this tribe may have sand only, while silica is completely absent from *Alpinia japonica*, *Burbidgea schizocheila* and *Elettariopsis curtisii*. Although not recorded in Table 1, silica sand, on the whole, is much less abundant in the tribes Hedychieae and Globbeae than in the Alpinieae, and it is completely absent from several species. The genus *Scaphochlamys* has an exceptionally large amount of silica sand.

Whilst the stegmata are very constant in their structure, and are therefore very useful for taxonomic purposes, the quantity of silica sand may vary in different samples of the same species, as indicated by S. & M. in *Alpinia speciosa*.

Costoideae

The genus *Costus* differs markedly from the rest of the family in the shape and distribution of its silica bodies: (i) The silica bodies of *Costus*, unlike those of the Zingiberoideae, are stellate or druse-like (Fig. 9m–o) and never granular or angular, the curves between adjacent projections being smooth. The cells in which they occur resemble typical stegmata, although individual cells may be rather large and elongated.

(ii) In *Costus*, unlike most Zingiberoideae, stegmata never occur in the epidermis, and are always adjacent to the vascular bundles. They are least common in the lamina, where they are occasionally absent (*C. lucanusianus*), and when present form part of the parenchyma of the bundle sheath. In the petiole, sheath, stem and rhizome stegmata are associated with most of the bundles, lying adjacent to the thick-walled fibres of the bundle sheath and often forming a complete layer around the bundle (Fig. 4h, *st.*).

Sand is infrequent in *Costus*, but in *C. lucanusianus*, it was seen to be abundant in the mesophyll and parenchyma sheaths of the bundle but decreased in quantity towards the base of the plant. Sand is completely absent from *C. malortieanus*. Silica is completely absent from the roots of all *Costus* spp.

From my own observations, and those recorded by S. & M., stegmata of the *Costus*-type have been found in all species of the genus so far examined. Therefore they are of considerable systematic importance, possibly for the whole subfamily, certainly for the genus.

(3) *Starch*

The following description of the starch grains, except where otherwise stated, is based on those from the rhizome. They are nearly always simple, but rarely appear to be compound with two or three hila (*Alpinia speciosa* (Fig. 9g)). The grains are often, but not exclusively, flattened, e.g. *Hedychium* (Fig. 9l), *Kaempferia* (Fig. 9h); in face view they are circular, oval, elliptical and slightly to very uneven in outline (*Hedychium*). The hilum is often situated in a projecting beak which may, or may not, lie in the plane in which the grain is flattened. Where the grains are flattened they may be disc-like (*Kaempferia*, Fig. 9h) or flake-like (*Hedychium*). Where the grains are not markedly flattened they may be spherical, cylindrical (*Elettaria*, Fig. 9f) or ellipsoidal. Striations arranged concentrically around the hilum are sometimes visible (Fig. 9h, l). The largest grains were those in the rhizome of *Costus lucanusianus*, the largest of which had dimensions of the order $40 \times 20\,\mu$ (Fig. 9j).

Starch is most abundant in the rhizome, although it was absent from this region in some species, e.g. *Kaempferia rotunda*. In the leaf lamina, very small, probably transitory grains are sometimes to be seen in the chloroplasts of the mesophyll; larger spherical grains are occasional in the parenchyma of the bundle sheath in the lamina, midrib and petiole (Fig. 4a, *k.*). In the leaf sheath, starch increases in quantity in the ground parenchyma, but only close to the bundles. Starch is more abundant in the cortex where it is again associated with the bundles, or, as in *Camptandra ovata*, confined to a region of the middle cortex corresponding to the chlorenchyma of the sheath. In

Table 1. *Distribution of silica in the subfamily Zingiberoideae*

A. Own observations

Tribe Alpinieae

Species	Steg-mata	Sand
Aframomum sp.	+	+
Alpinia javanica	+	+
A. bracteata	+	+
A. sanderae	−	+
A. speciosa	+	+
Burbidgea schizocheila	−	−
Catimbium latilabre	+	+
C. speciosum	+	+
Elettaria cardamomum	+	+
Elettariopsis curtisii	−	−
Geostachys taipingensis	−	+
Hornstedtia conica	−	+
H. scyphifera	+	+
Renealmia sp.	+	+

Tribes Hedychieae and Globbeae

Species	Steg-mata	Sand
Hedychieae		
Brachychilum horsfieldii	−	+
Camptandra ovata	−	−
Cautleya spicata	−	+
Curcuma sp.	−	+
C. domestica	−	−
Hedychium coccineum	−	+
H. elatum	−	−
H. gardnerianum	−	+
H. malayanum	−	+
Kaempferia angustifolia	−	−
K. gilberti	−	−
K. kirkii	+	−
K. rotunda	−	+
Roscoea cautleoides	−	−
R. humeana	−	−
R. purpurea	−	−
Scaphochlamys breviscapa	−	+
S. erecta	−	+
S. rubromaculata	−	+
Zingiber officinale	−	+
Globbeae		
Globba bulbifera	−	+
G. winniti	−	+

B. Observations recorded by Solereder & Meyer

Species	Steg-mata	Sand
Alpinia allughas	+	+
A. calcarata	.	+
A. japonica	−	−
A. mutica	.	+
A. speciosa	+	+
Donacodes pininga	+	.
Elettaria cardamomum	+	+
Phaeomeria magnifica	+	+
Renealmia exaltata	.	+
Genera only		
Amomum	−	.
Renealmia	−	.

Species	Steg-mata	Sand
Hedychieae		
Hedychium gardnerianum	.	−
Kaempferia rotunda	.	+
Zingiber casumnar	.	+
Globbeae		
Globba bulbifera	.	+
Genera only		
Hedychieae		
Brachychilum	−	.
Cautleya	−	.
Curcuma	−	.
Hedychium	−	.
Hitchenia	−	.
Kaempferia	−	.
Roscoea	−	.
Zingiber	−	.
Globbeae		
Globba	−	.

general, starch is uncommon or inconspicuous in the aerial parts. In the rhizome, starch is often concentrated around the endodermis in the inner cortex and outer layers of the central cylinder; the endodermis itself is always starch free. Starch is infrequent in all but the storage roots, where it may occupy the cortex, pith or both.

Although flattened starch grains are said to be characteristic of the Scitamineae, they are by no means universal, in many species the grains show no signs of flattening. The shape of the grains, however, appears to be constant and characteristic for certain genera, e.g. *Alpinia*, *Costus*, *Hedychium* and *Kaempferia*. It may also be diagnostic for the species, since MacFarlane (1892) has shown how the size and shape of the starch grains in the hybrid between *Hedychium gardnerianum* and *H. coronarium* are intermediate between those of the starch grains in the parents.

(4) *Tannin*

Substances included under the comprehensive term 'tannin' are very frequent in all species of the Zingiberaceae. Two extreme types of tannin cell may be recognized, although there may be transitions between them. In the first type tannin completely fills the cell lumen and has a dark or golden-brown homogeneous appearance. Cells of this type are very characteristically associated with the vascular bundles and often form connected series adjacent to the parenchyma of the bundle sheath. These cells were conspicuous in the aerial parts of the available material of *Zingiber officinale* where they were much elongated with only occasional septa, forming tubes which resemble laticifers. Tannin of this type was found occasionally in xylem vessels and in hairs of the leaf margin.

In the second type the tannin appears to be limited to the protoplasm of the cell and is always very dark in colour (Fig. 8f). Often the protoplast has a convoluted appearance as if invaginated in numerous places and, where the protoplast is not separated from the cell wall and the invaginations are few and large, the cell looks as if it contains tyloses (Fig. 8g). Very rarely, in sections treated with phloroglucin and concentrated HCl, the contents of cells of this type assume a pink colour and it was thought that the tannin was giving a lignin reaction. However, since the colour change is given in acid alone, it is possible that the tannin cells themselves contain phloroglucin. This reaction was given in a few cells only in a particular region, in *Alpinia speciosa* (upper part of the leaf sheath), *Cautleya spicata* (rhizome) and *Scaphochlamys breviscapa* (sheath). Other tannin cells in the same section remained unchanged.

Tannin cells of the second type differ little in form from neighbouring cells. In the mesophyll the tannin cells are often larger than normal chlorenchyma cells (Fig. 21, *t.*). Where tannin completely fills the cell lumen it may penetrate the pit-cavities, providing a very convincing demonstration of these structures, as in the cells adjacent to the endodermis in *Alpinia sanderae*.

Tannin rarely occupies an extracellular position. It was found in the intercellular spaces in the petiole of *Zingiber officinale* and the root cortex of *Kaempferia kirkii*. It is interesting to note that in the latter species tannin was absent from all other organs.

Two types of tannin deposit, probably corresponding to those described above, were distinguished by Barthelat (1893). From my own observations and those recorded in the literature the distribution of tannin is evidently a very variable feature. Consequently, tannin substances offer no diagnostic features within the family. The chemistry and significance of these deposits remains almost entirely unknown.

OIL CELLS AND ABORTED STOMATA

Zingiberoideae

The techniques used to identify oil cells are described in the earlier section on material and methods. Of the material available, the oil cells in *Hedychium gardnerianum* were studied in greatest detail. In fresh material of the leaf they are visible in sections as spherical cells each containing a refractive body ('resin body') (Fig. 9e). There may be a single body almost filling the cell lumen, or several smaller bodies. These may be released in sectioning so that the oil cells often appear empty. In material fixed in FAA or 70 per cent alcohol, the contents often appear unaltered, but generally the resin body assumes a more granular, amorphous appearance. One distinct variation is the stellate, druse-like shape of the body in certain species, probably due to crystallization (Fig. 9*a*), another is for the contents to be pale yellow, globular and like a simple oil drop. Sudan IV stains the resin body a bright orange, and may be used for a rapid detection of these cells. The resin bodies disappear in permanent Canada balsam mounts.

The characteristic feature of these cells is the suberization of their walls, and tests with chlor-zinc-iodide or I_2KI and sulphuric acid are used to detect this (see p. 552). The suberin cannot be detected with Sudan IV, although a little safranin is retained in permanent preparations. Differentiation of the wall into distinct lamellae could not be recognized.

The oil cells are at first spherical, but may become somewhat cubical owing to the pressure of surrounding cells (Fig. 9c). In *Hornstedtia scyphifera* the oil cells of the mesophyll were elongated in the anticlinal direction, when they resembled palisade cells in shape. Where oil cells occur in the hypodermis they resemble the neighbouring cells in shape, but are slightly smaller. Where oil cells occur in the epidermis they are distinguished in surface view by their isodiametric shape and smaller size (Figs. 9b; 2h, *o.c.*). In section, epidermal oil cells are generally recognized by their smaller size (Fig. 9d) and frequent conical projection into the hypodermis (Fig. 9a). Typical measurements of the average diameter of oil cells in the mesophyll are 16·0 μ for *Kaempferia gilbertii*, 35·7 μ for *Roscoea cautleoides* and 51·8 μ for *Hornstedtia conica*.

A variable number of oil cells have been observed or reported to be present in all species of the subfamily Zingiberoideae so far studied. In the lamina they are most conspicuous in the mesophyll, where they most often occur in the layer between palisade and spongy tissue (Fig. 2j, *o.c.*). Oil cells may also be present in the leaf hypodermis (*Brachychilum horsfieldii*, *Scaphochlamys* spp. and several genera reported by S. & M.). In my preparations they were also frequent in the lower epidermis where they were easily recognized in surface view, e.g. in species of *Aframomum*, *Alpinia*, *Brachychilum*, *Camptandra*, *Elettaria*, *Globba*, *Hedychium*, *Hornstedtia*, *Kaempferia* and *Roscoea*. Epidermal oil cells have also been recorded by S. & M. in species of the following additional genera —*Amomum*, *Cautleya*, *Curcuma*, *Donacodes*, *Phaeomeria*, *Renealmia* and *Zingiber*. S. & M., however, record the occurrence of epidermal oil cells in species in which I have not seen them. This suggests that the presence of oil cells in the epidermis may be a variable feature. Oil cells in the upper epidermis have been seen only in species of *Kaempferia*, in which genus they have also been recorded by S. & M.

Where oil cells are present in the epidermis of the lamina, they generally occur also in the epidermis of petiole and sheath. In the internal tissues of the petiole and sheath the oil cells tend to be associated with the chlorenchyma surrounding the air canals, but they become progressively more frequent in the ground parenchyma towards the base of the sheath. Oil cells are less common or absent in the aerial stem. In the rhizome and root they are numerous and in the root they may be limited to the cortex. Oil cells are conspicuous because of their isodiametric shape when the surrounding ground parenchyma consists of elongated cells (Fig. 9c).

The number of oil cells varies considerably in different species or in individuals belonging to a single species, as indicated by Meyer (1881) for *Curcuma*; also in different parts of the same plant.

Aborted stomata

Futterer and S. & M. all report the occurrence in the lower epidermis of the lamina of small cells which are 3 to 4-sided or rounded in surface view, and which they interpreted as aborted stomatal initials. These were occasionally seen in my own material. In surface view they are practically indistinguishable from epidermal oil cells, though they are more variable in shape and size. The only reliable method for distinguishing them from oil cells is the I_2KI-H_2SO_4 test in which, unlike true oil cells, they show the blue of normal cellulose walls. By this technique they were demonstrated by me in *Globba bulbifera*, *G. winniti*, *Kaempferia kirkii* and *Roscoea purpurea*. Their occurrence is evidently sporadic. Although they are reported in the literature to be present in *Zingiber officinale* (Futterer), *Alpinia speciosa* and *Hedychium gardnerianum* (S. & M.), I was unable to confirm this.

Costoideae

The oil cells which are so conspicuous a feature of the Zingiberoideae are completely absent from *Costus* and are reported to be absent from *Tapeinochilos*. It is therefore reasonable to assume that they are absent from the whole of the subfamily Costoideae. This probably explains why this subfamily lacks the aromatic odour which is so characteristic of the Zingiberoideae. The presence of oil cells is reliable for diagnostic purposes, however, only in a positive sense. This is because they are difficult to detect in some of the Zingiberoideae and may easily be overlooked.

Further discussion on the subject of oil cells is given on p. 585.

Histology of the vascular tissues

(1) *Xylem elements*

Because the occurrence and distribution of tracheids and vessels is of considerable phylogenetic interest, the tracheal elements have been examined in some detail. The maceration techniques used in the study of these elements have been described under ‘Material and Methods’.

The presence or absence of a perforation in the end wall can be observed in unstained elements orientated so that the end wall is seen in optical longitudinal section (Fig. 10a, e). Microchemical methods were inconclusive. Vessels can be recognized by the narrow bars of the scalariform perforation plates which are not bordered, while on imperforate walls the bars are wider and slightly bordered. Perforated walls can also be recognized because, owing to the absence of a primary membrane, the bars are supported only at their ends and consequently tend to be unevenly spaced in the centre. These criteria are similar to those used by Fahn (1954) to distinguish vessels from tracheids.

In describing the inclination of the end walls the same terms have been used as those previously adopted by Cheadle (1943*a*). Thus the end wall is said to be transverse when it lies at right angles to the length of the element, to be slightly oblique when it is not more than twice as long as the diameter of the element, oblique when two to five times the diameter and very oblique when more than five times the diameter.

In the material examined vessels were confined to the roots, elsewhere tracheids only were present. In the leaf lamina, the thickenings of the tracheids consist of up to twelve helically wound bands and the end walls are very oblique or ill-defined. There is a gradual transition towards the scalariform tracheids of the rhizome and root, the level at which transitional types are to be found is very variable and they may be present even in the stem or the leaf sheath. In the rhizome the angular tracheids are often irregular, occasionally forked and may very rarely show a ‘tail’. Elsewhere tracheids are either circular or slightly polygonal in section when each facet of the polygonal type corresponds to a xylem parenchyma cell. The pits which form the scalariform sculpturing of imperforate walls are inconspicuously bordered, the thickening bands, as seen in optical section, being thinnest towards the primary wall, to which they are often attached by a narrow beak (Fig. 10g). In the root, where fibres of the ground tissue abut on the lateral walls of tracheids and vessels, the area of contact is unpitted (Fig. 10b, c).

While the end walls of tracheids vary from oblique to very oblique, or are even unrecognizable, the perforation plates of the vessels in the root vary from oblique to transverse. The perforation plates are scalariform with few (Fig. 10b) to many (Fig. 10a) bars. Simple, generally transverse perforations were seen frequently in *Elettaria cardamomum* (Fig. 10c), and uncommonly in *Elettariopsis curtisii* and *Catimbium latilabre*. The perforation plates are often convex, and encroach into the lumen of the adjacent element of the vessel, the complementary end wall of which is correspondingly concave. The two end walls of a single element are generally similar, but occasionally markedly different. One may be oblique, the other transverse and, in one example, an element had a slightly oblique perforation plate at one end and a very oblique, imperforate termination at the other.

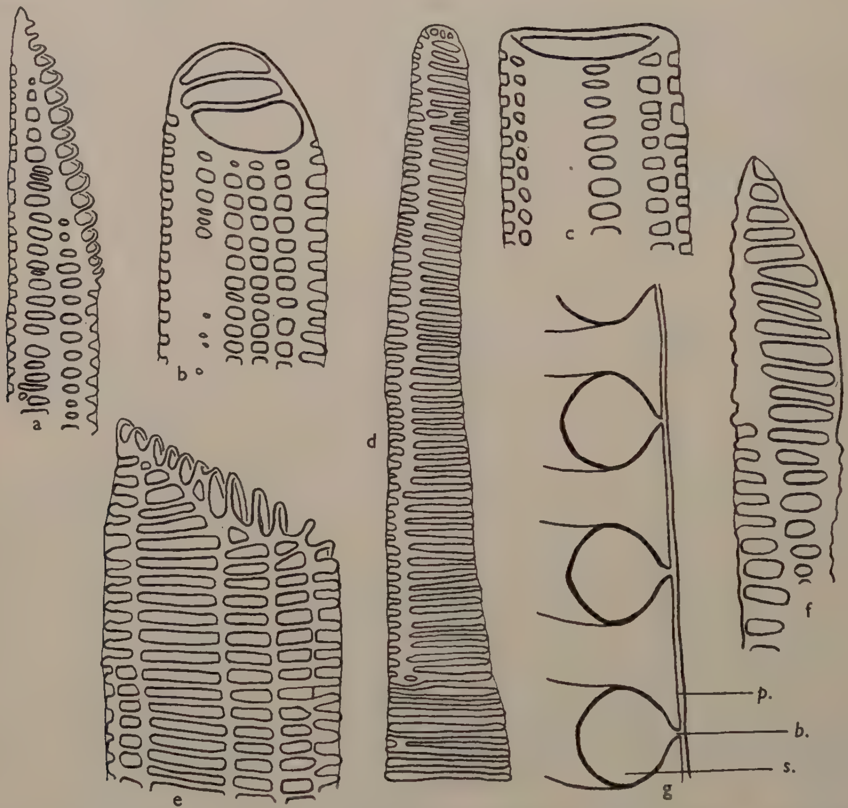


Fig. 10. Xylem elements from the root. (a) *Costus tappenbeckianus*, vessel (× 292). (b and c) *Elettaria cardamomum*, vessels (× 292). (d) *Hedychium gardnerianum*, tracheid (× 200). (e) *Catimbium latilabre*, vessel (× 270). (f) *Hedychium gardnerianum*, vessel (× 270). (g) Diagram showing attachment of secondary thickening bars (*s.*) to primary wall (*p.*) of vessel, by means of 'beak' (*b.*).

Within a single root the type of xylem element may be roughly correlated with its time of development. The first formed elements are very long, narrow tracheids with very oblique, imperforate end walls (Fig. 10d). Of the later maturing elements, those that differentiate successively towards the centre of the root are shorter and wider and their end walls more specialized and finally the innermost elements, which are the largest and the last to be formed, are generally vessel members. These may be very short, e.g. in *Elettaria* they were only three to four times as long as wide. As the last elements to be formed in the root are very late in maturing, no vessels are to be seen in material close to the root apex. Where the protoxylem of the root differentiates in a region which has not ceased to elongate, it is extended and obliterated by encroachment of the surrounding xylem parenchyma cells, although the persistent annular thickenings are often encountered in transverse sections. A transition from this condition to the ballooning of pit-membranes to form tylose-like invaginations has already been mentioned for other organs (p. 559). The tracheal elements, especially in the underground parts, may contain tannin deposits. Large crystals were observed filling the tracheids of the stem in *Aframomum* sp. and *Brachychilum horsfieldii*.

(2) *Phloem elements*

Only incidental observations were made on the phloem tissue. The phloem consists of sieve-tube elements which are the widest cells; companion cells distinguished by their small size and densely staining contents; and phloem parenchyma. The parenchyma becomes lignified and thick-walled in certain regions in *Hornstedtia* spp. (p. 559). The phloem elements towards the xylem are small and often apparently undifferentiated, possibly consisting of residual procambium. Tannin is not infrequent in the phloem elements while crystals are rare.

The sieve-tube elements are long and narrow, the widest to be measured were those in the stem of *Hornstedtia conica* with an average diameter of 13 μ. The sieve plates are always simple and the pores are very minute. Using the same terminology as Cheadle & Whitford (1941), which corresponds to that used in describing the xylem elements, the sieve plates are transverse to slightly oblique in the aerial parts; in the roots they are more inclined, but may vary from transverse to oblique.

The phylogenetic implications of these observations on the conducting elements are discussed later.

Discussion of some histological details

Since a very broad survey of the vegetative anatomy of the Zingiberaceae has been attempted, several problems of detailed histology which have been raised have not been fully clarified. Of these, the oil cells and the 'stegmata' are most important. Evidently these structures require much closer examination, and the problems raised are therefore indicated here; the literature relevant to them is summarized and discussed, in the hope that this will stimulate further research. A discussion of the phylogeny of the conducting elements is also included here, in view of the current interest in this subject in the Monocotyledons.

(1) *Oil cells*

De Bary was first to notice that the walls of certain resin-containing cells in several families, including the Zingiberaceae, turned yellow in I_2KI and concentrated sulphuric acid, in contrast to the blue of normal cellulose walls. These cells—oil cells or 'secretory-sacs' ('Sekretbehälter')—have been studied in some detail by Biermann (1898) and Zacharias (1879) and for the Zingiberaceae alone, by Barthelat (1893).

The first peculiarity of these cells is that they differentiate very early. In the meristematic tissues of the shoot and root apices the oil cells are very conspicuous because they are much larger than the surrounding, undifferentiated cells. Later on, the cells of the ground tissue expand and become larger than the oil cells.

Probably these oil cells play some important function in the physiology of the plant. However, the early speculation that the oil cells serve only for secretion of waste material, has not been modified or even discussed in recent years, and therefore needs serious investigation.

Secondly, there are differences of observation on the structure of the wall in these cells. All of the early workers recognized at least two lamellae in the walls of the oil cells of which the outer is suberized and the inner is of cellulose. Causing them to swell in cold, 10 per cent KOH solution and staining with chlor-zinc-iodide was claimed to be the best treatment for demonstrating these wall lamellae. However, in none of my preparations using this technique could two lamellae be clearly distinguished. That there may be small differences in the oil cells within the Zingiberaceae is indicated by Biermann (1898), who records that the walls of the oil cells in *Hedychium gardnerianum* on one hand and those of *Curcuma zedoaria* and *Zingiber officinale* on the other were slightly different. Variations in the quantity and even quality of the contents in different samples of the same species have been recorded by Petersen (1889) and Schumann (1904).

A final consideration is that the oil cells are probably the source of many substances which make members of the Zingiberaceae commercially important. This is indicated by the restriction of oil cells to the Zingiberoideae, and members of this subfamily only are aromatic. The subfamily Costoideae are completely without oil cells and, in the aerial parts at least, are not aromatic. Curcumin, the principle of turmeric, is limited to certain 'curcumin-cells' and this imparts the distinctive yellow colour to the rhizome of *Curcuma domestica* Valet = *C. longa* Koenig. Chemical analysis of the contents of the oil cells would be of general interest.

(2) '*Stegmata*'

As indicated earlier (p. 576), the descriptive terminology for silica bodies is still in need of clarification. The term stegmata is here applied to isodiametric or slightly elongated cells containing silica bodies. These occur in longitudinal series that always lie parallel and adjacent to the fibres of the bundle sheath or fibre cylinder.

Netolitzky (1929) applied the terms 'stegmata' and 'Deckzellen' to cells of which each contains a silica body (or calcium oxalate crystal), the cells themselves being arranged in files which lie next to, and parallel with, fibres. They are said to develop from prosenchymatous elements which undergo transverse divisions, silica bodies developing in each daughter cell. The wall adjacent to the fibre is thickened and partly envelops the silica body, the thinnest point in each cell wall being most remote from the adjacent fibre.

In the Zingiberaceae S. & M. describe five types of silica-bearing cell, but they only consider those in *Alpinia allughas* (and possibly *Donacodes pininga*) to be true stegmata. The comparable cells in other species are said to lack the wall thickenings that are supposed to be characteristic of true stegmata. Despite this opinion, however, it should be noticed that S. & M.'s illustrations of the stegmata of *Alpinia allughas* do not show any of the thickenings that they hold to be an essential characteristic of these cells. In my opinion, it is undesirable to define stegmata on the nature of the wall thickenings while ignoring the characteristics of the silica bodies themselves.

In the sense now proposed, in the Zingiberaceae, the term stegmata would therefore include the first of three of the five types of silica-bearing cell recognized by S. & M., i.e. that shown by *Costus*, by *Alpinia allughas*, by *Elettaria* and other species.

(3) *Evolution of the vascular elements*

As a result of observations on the different types of tracheal elements throughout the plant and within each organ of the plant in Monocotyledons, Cheadle (1953 and earlier papers) has come to several conclusions concerning the phylogeny of these elements. My observations on the Zingiberaceae support these conclusions. The first is that in the Monocotyledons, specialization of the xylem elements began first in the roots, from whence it spread, via the rhizome, to the aerial parts (Cheadle, 1943*b*). I also agree with Cheadle that in most of the Zingiberaceae, vessels are confined to the roots only, and he records them for the stem with certainty only in *Dimerocostus uniflorus* and *Renealmia strobifera* (Cheadle, personal communication). The Zingiberaceae are evidently a relatively primitive family so far as their tracheal elements are concerned.

Cheadle's (1944) further conclusion that, within each organ, the specialization in the late metaxylem preceded that in the early metaxylem, is supported by observations on the root.

S. & M. record but little information concerning the xylem elements. They refer to scalariform perforations in *Globba maranta* and simple perforations in *Alpinia speciosa*. *Hedychium gardnerianum* is recorded as having tracheids only, and this is commented upon by Cheadle (1953, p. 37) as, if it were true, it would mean that this species is the only Monocotyledon, apart from certain specialized aquatics, from which vessels are known to be absent. In the present investigation true vessels with scalariform perforation plates were frequently observed in the roots of *H. gardnerianum* (Fig. 10e). Therefore it is probable that the material to which S. & M. refer was too young for its vessels to have developed, since it has been indicated above that the earliest formed xylem elements in any organ are the most primitive, i.e. are tracheids, and that the last formed elements mature very late.

Since in many Monocotyledons the types of xylem element can be arranged in a series to show the transition from tracheids to vessel, and in order to call attention to this transition, Fahn (1954) has recently suggested that intermediate types should be distinguished by the name vessel-tracheid. This term would then apply to elements which resemble tracheids with their very oblique end walls with numerous scalariform bars, but with perforations between the bars, as in vessels. Vessel-tracheids would then be fairly common in the Zingiberaceae.

The few observations made on the sieve-tube elements, while indicating that there is great uniformity in them in the Zingiberaceae, do not contradict the conclusion of Cheadle & Whitford (1941) that in the Monocotyledons generally, the most specialized sieve-tube elements are to be found in the leaf and the least specialized in the root.

Summary and discussion of taxonomic conclusions

(1) *Differences between the subfamilies Zingiberoideae and Costoideae*

(a) *Anatomical differences*

It is already well recognized that the subfamily Costoideae, as represented by *Costus*, is very distinct in its morphology from the remainder of the family. The present investigation has served to indicate how *Costus* is also very distinct from the rest of the family in its anatomy, and these conclusions are summarized in Table 2.

Although *Costus* was the only genus in the Costoideae that I was able to examine, the few facts recorded in the literature concerning the anatomy of the other three genera in this subfamily agree with my own observations on *Costus* itself. It therefore seems reasonable to assume that the characteristics that serve to distinguish *Costus* from the Zingiberaceae are equally diagnostic for the Costoideae as a whole.

(b) *Other differences*

Taxonomy should be based on evidence from as many disciplines as possible in the final evaluation of its units, and it is therefore necessary to consider what other evidence exists to indicate that the Costoideae constitute a distinct and natural group. This evidence, which has been taken from the literature, is summarized in Table 3, with further elaboration below.

Morphology. Apart from the well-known differences of vegetative and floral organization in the two sub-families, there is a suggestion by Troll that the labellum of *Costus* may be fundamentally dissimilar to that of the Zingiberoideae. In view of the larger size of the labellum of *Costus*, Holttum (1950) considers that this suggestion may well be true.

Geographical distribution. Details of the distribution of members of the two subfamilies are given on p. 550.

Seedling development and structure. Besides the marked differences between the two subfamilies in seedling structure which have been revealed by the studies of Boyd (1932), *Costus* shows a unique feature compared with monocotyledonous seedlings as a whole. Thus, at the apex of the lamina, where the tip of the cotyledon enters the seed, there arises a small, spherical, non-vascular outgrowth or plug, which, on germination, is withdrawn from the seed.

Table 2. *Summary of anatomical differences between the Zingiberoideae and Costoideae*

	Zingiberoideae	Costoideae
(1) *Leaf*		
Epidermis (surface view)	Cell files and subsidiary cells of stomata generally regular. Cells above main veins modified	Cell files and subsidiary cells less precise. Cells above veins not modified
Hypodermis	Generally moderately developed, may be well-developed (e.g. *Scaphochlamys*) or absent (e.g. *Camptandra*)	Always well-developed either in number of cell layers or cell size. (Proportion of assimilating tissue relatively small)
Vascular bundles (veins)	At least the largest bundles connected to the epidermis by bundle sheath extensions. (Sometimes bundles completely independent of epidermis, e.g. *Scaphochlamys*, *Camptandra*)	Leaf bundles never connected to the epidermis by extensions of bundle sheath
Midrib (standard level)	Main bundle arc towards *abaxial* surface. Subsidiary arcs, when present, one upper or one lower or both one upper and one lower. (Sometimes midrib region with a single bundle, e.g. *Camptandra*)	Main bundle arc towards *adaxial* surface. Subsidiary arcs represented by a single median, abaxial bundle
Petiole	Maximum of four bundle arcs, main arc (I) close to *abaxial* surface. Subsidiary arcs, two above, one below main arc, if all present. Bundle sheaths of fibres, collenchymatous development of bundle sheaths very rare (*Zingiber* spp.)	Maximum of four bundle arcs, main arc (I) towards *adaxial* surface. Subsidiary arcs all below main arc. Bundle sheaths always of collenchyma
Sheath	Main arc not pectinated with subsidiary arc. Abaxial subsidiary arc (II) progressively stronger towards base of sheath. Adaxial subsidiary arcs (III and IV) progressively reduced towards base of sheath	Main arc and subsidiary arc pectinated to form a single cylinder, plus single, median abaxial bundle
Air canals	May extend from base of sheath to midrib of lamina	Never extend into petiole, confined to base of sheath
(2) *Stem*		
T.S. internode	Cortex generally wide. Fibre cylinder entire, circular in section. Cortical bundles never in contact with fibre cylinder	Cortex narrow. Fibre cylinder undulate in section. Cortical bundles in contact with fibre cylinder
T.S. node (associated with course of bundles in the stem)	No nodal plexus developed. (No branching of the aerial stem)	Nodal plexus developed. (Axillary buds and branching in the aerial stem)
(3) *Hairs*	Often slightly to markedly (*Hornstedtia*, *Renealmia*) sunken. Always unicellular (except for two-celled hairs on stem of *Curcuma*)	Never sunken. Frequently multicellular (uniseriate)
(4) *Silica*	Stegmata (tribe Alpinieae): confined to lamina, always dermal (except *Hornstedtia*). Silica body spherical, surface irregular (granulose)	Stegmata: found in leaf and aerial stem, never dermal. Silica body stellate, druse-shaped, surface smooth
(5) *Oil cells*	Present in all parts. (Plants aromatic)	Completely absent. (Plants not aromatic)

Pollen structure. Because of the thin extine in the pollen grains of the Zingiberoideae, after the standard acetolysis technique used by Erdtman (1952) in his palynological studies, the grains are left in a shrivelled and wrinkled condition. They therefore require an after-treatment by boiling in a 5 per cent potassium hydroxide solution to restore them (Erdtman, p. 9). The pollen grains in those members of the Costoideae which have been studied (*Costus*, *Tapeinochilos*) have a thick extine, resistant to acetolysis. It is interesting to note that the remaining families of the Scitamineae—Cannaceae, Marantaceae and Musaceae, all require the same after-treatment as the Zingiberoideae. Therefore, in their pollen structure the Costoideae are distinct not only from the rest of the Zingiberaceae, but from the Scitamineae as a whole.

Table 3. *Summary of other differences between the Zingiberoideae and Costoideae*

	Zingiberoideae	Costoideae
(1) Morphology		
(*a*) Vegetative (Holttum, 1950)	Aerial stem unbranched, pseudostem most conspicuous part of shoot. Leaves distichous. Leaf sheaths long, open	Aerial stem branched, true stem well-developed. Leaves spirally arranged, with divergences, 1/5, 1/6, 1/7, ..., etc. Leaf sheaths short, closed (tubular)
(*b*) Floral (Holttum, 1950)	Lateral staminodes usually present, often small. Stylodes (nectar glands) various, always ± columnar, sometimes absent	Lateral staminodes absent. Stylodes absent, nectar glands embedded below base of flower tube
(*c*) Labellum (Troll—see Loesner, 1930)	Consists of *three* non-functional stamens	Probably consists of *five* non-functional stamens. Large and convoluted
(2) Geographical Distribution (Loesner, 1930)	Centre of distribution in Indo-Malaya	Centre of distribution in Central America
(3) Seedling Development and Structure (Boyd, 1932)	Germination hypogeal, cotyledon acts as an haustorium, only ligule well-developed. Two vascular strands in cotyledon	Germination epigeal, cotyledon lamina well-developed. Five vascular strands in cotyledon
(4) Pollen Structure (Erdtman, 1952)	Non-aperturate. Extine thin, not resistant to acetolysis (requires after-treatment)	Aperturate. Extine thick, resistant to acetolysis (no after-treatment required)
(5) Cytology (Raghavan & Venkatasubban, 1943)	Basic number, $x=12$ (*Alpinia*, *Elettaria*, *Globba*, *Kaempferia* and *Phaeomeria*). $x=11, 12$ (*Zingiber*); $x=21$ (*Curcuma*); $x=9, 17, 26$ (*Hedychium*)	$x=8, 9$. $2n$ values of 16, 18, 36.

Cytology. Raghavan & Venkatasubban (1943) conclude that the chromosomes of *Costus* are distinctive, not only in number as indicated in Table 3, but also in morphology, and these facts would justify the separation of the genus into a distinct group.

Just how far these conclusions, based largely on *Costus*, can be applied to the Costoideae as a whole will only be revealed by future research. For the present it is assumed that the results obtained with *Costus* are equally applicable to its related three genera. The whole of the evidence quoted above indicates that the Costoideae are a distinct and natural group. Indeed, they not only form a distinct subfamily but show features not found in the remaining members of the Scitamineae.

Hutchinson (1934) has expressed the opinion that *Costus* and related genera should be given the status (Costeae) of a tribe equivalent in rank to the other tribes into which he divides the Zingiberaceae. The present study suggests that this is too cautious a view, and that the group should certainly be treated as a subfamily, possibly even a family.

(2) *Differences between the tribes within the Zingiberoideae*

With the exception of the type of silica inclusion, there are no anatomical features which consistently serve to distinguish the tribes Globbeae, Hedychieae and Alpinieae into which the subfamily Zingiberoideae is divided. The distinction based on the silica inclusions also is not absolute. The Alpinieae mostly have the type of silica-bearing cells which have here been termed stegmata, while the Globbeae and Hedychieae, with a single exception (*Kaempferia kirkii*), never possess stegmata (Table 1). Deposits of silica sand are more frequent and abundant in the tribe Alpinieae.

That the tribes are natural groups, however, is indicated by the work of Weisse (1932, 1933) on the type of distichy in the Zingiberaceae. Weisse found that the shoots arising in the axils of the lowest scale leaves at the base of the upright stems (i.e. the renewal buds, (p. 547), could be divided into two types according to the plane of insertion of the distichously arranged leaves. Either the plane of insertion is parallel with the direction of the rhizome (median distichy) or is perpendicular to this direction (transverse distichy). It was found that the tribes Globbeae and Hedychieae show median distichy. The tribe Alpinieae, on the other hand, shows transverse distichy, with the exception of the genus *Zingiber* which has median distichy. Evidently *Zingiber* has a more natural position in the first group, where it has already been placed by Holttum on other grounds (p. 549). At the time when he made this change Holttum (personal communication) was unaware of this early work which supports his views so well.

The combined evidence from floral and vegetative morphology and anatomy indicates that the tribe Globbeae has closer affinities with the Hedychieae than with the Alpinieae.

(3) *Anatomical differences between the lower taxonomic units*

A peculiarity of the anatomy of the Zingiberaceae, approached from the systematic view point, is that while the various tribes cannot be separated on anatomical grounds, the genera often show structural features by which they may be recognized. Genera appear to be delimited in the following three ways:

(i) Features which are present throughout the family may in their variation delimit certain genera. For instance, the appearance of the midrib, petiole and sheath in transverse section is often somewhat constant and characteristic for the genus, as in *Alpinia*, *Globba*, *Hedychium*, *Kaempferia*, *Roscoea* and *Scaphochlamys*. This depends largely on the arrangement of the vascular bundles and their degree of development at different levels.

The shape of the starch grains may also characterize certain genera.

(ii) There are certain structures which occur very rarely and then appear to be confined to a single genus. The sclerification of phloem parenchyma cells in the aerial parts is limited to *Hornstedtia*; the well-developed hypodermis and palisade-like layer of assimilating tissue abaxial to the spongy mesophyll in the lamina distinguishes the genus *Scaphochlamys*; the large calcium oxalate crystals in the lower hypodermis may be diagnostic for *Globba*. Internal stegmata, otherwise absent from the Zingiberoideae, are recorded for some species of *Hornstedtia* only.

(iii) Certain features may be conspicuous in a single genus. Examples are the sunken, bulbous-based hairs on the lamina of *Hornstedtia* and *Renealmia*, and the isolated phloem groups in the central ground tissue in the root of *Hedychium*. Fibre groups independent of the bundle sheaths are probably characteristic of the lamina of *Renealmia*, but also occur in other genera, e.g. *Aframomum*.

Unfortunately, these conclusions relating to genera can only be regarded as tentative, since the constancy of these diagnostic features can only be determined by the examination of a much larger number of species in each genus than has already been done. In addition, the delimitation of genera by traditional taxonomic methods is by no means complete, as indicated by the recent valuable work of Holttum. The whole family evidently requires detailed systematic revision, and this is further complicated by the presence of hybrids.

At the specific level anatomical differences are largely quantitative.

GENERAL SUMMARY

Forty-one species of the Zingiberaceae have been studied from the standpoint of systematic anatomy.

The two subfamilies, Costoideae and Zingiberoideae, into which the Zingiberaceae is divided, differ markedly in the anatomy of the lamina, petiole and sheath; the structure of the node in the aerial stem; the structure of the hairs, and in the type and distribution of silica inclusion. Oil cells are found only in the Zingiberoideae.

The anatomical evidence for the separation of the two subfamilies is supported by evidence from vegetative and floral morphology, geographical distribution, pollen, seedling structure and cytology.

The tribes within the Zingiberoideae can be distinguished only in the plane of insertion of the leaves and the type of silica cell. Individual genera, however, frequently show a characteristic anatomy.

Observations on the types of conducting element in the xylem and phloem support current theories concerned with the phylogeny of these elements.

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On certain planktonic palmelloid green algae. By J. W. G. Lund, Freshwater Biological Association, Ambleside.

(With 9 Text-figures)

[Read 19 January 1956]

There is a large number of planktonic algae which are commonly considered to be palmelloid members of the Volvocales (sensu Fritsch, 1935). Many have been grouped together erroneously in the past in the genera *Gloeocystis* Naeg. and *Sphaerocystis* Chod. (*Gloeococcus* of some authors). Moreover, in preservatives, the characters which distinguish them are often lost,[1] so that very little reliance can be placed on many records.

After Smith's (1920) account of those in the Wisconsin plankton, little advance was made until the recent works of Teiling (1942, 1944, 1946) and Skuja (1948). None of these workers grew the algae in culture. Desirable though this is, great care must be taken to ensure that the growths are not peculiar to the laboratory media and conditions. Most of these algae are capable of considerable changes in appearance. Indeed, most or all can be cultivated on agar to produce what are subaerial growths which bear no obvious resemblance to those seen in the plankton. These growth forms, and those in old liquid cultures or in inorganic or partly organic media with relatively high concentrations of salts (e.g. Knop and Benecke solutions), are often such that taxonomically distinct algae appear to be identical and descriptions of such stages are usually of little value. Indeed, they may be harmful in that they lead to incorrect nomenclature and to prejudice against the use of cultures. Such growths have also been used to separate species as was done to some extent by Chodat (1913, 1926, see also Fritsch in Pringsheim 1946, p. vii), particularly when, as in his case, it is not certain that his cultures were really all under the same conditions or sampled at identical intervals of time. Even when the features described do reflect genetical differences, these may be such that erection of new species is scarcely justified. There is a danger that, having reached a viewpoint similar to that of a shepherd who sees marked differences between the sheep in his flock (a sheep no doubt sees even greater ones), a new taxon is made for each isolation. Since, for these and many other algae, we do not yet know what genetical differences control the morphological ones we can observe, it seems best to use primarily the classical morphological methods of taxonomy. Where clone cultures are used for special investigations, such as physiological experiments, they are best catalogued by numbers or other convenient symbols after the specific or other name.

I have, however, used some clone cultures, for by this means one can be sure that the material is homogeneous. It is then possible to see how two algae, which may appear to some to be doubtfully distinct from the descriptions of natural populations, do grow and behave under identical conditions. Thus, as will be seen, *Paulschulzia pseudovolvox* (Schulz) Skuja and *P. elegans* (Woron.) Lund always react and grow in certain different ways in culture, even though, in the latter species, it is difficult to produce plants identical in all respects with the natural stock from which the isolations were made. Support is thus produced for their separation on the morphology of natural populations, some of whose members may seem to resemble each other rather closely. In addition, of course, cultures are essential for obtaining experimental data to support or disprove views on the ecology of algae based on observations in nature.

The cells of all the algae described here are embedded in mucilage which may or may not take up stains. Even if it does, the stains nearly always lead to more or less marked contraction. Hence, these algae are best observed alive, mounted in indian ink or under phase contrast.

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[1] An exception is the pseudocilium which generally becomes easier to see on prolonged preservation in weak formalin.

(1) **Radiococcus planktonicus** sp.nov. (Fig. 1 A–C)

The globose cells (4–7 μ diam.) are distributed at random within the colony (to 250 μ length), which is more or less globose when small and of irregular but rounded outline when large. The mucilage is structureless, nor is there any separate investment

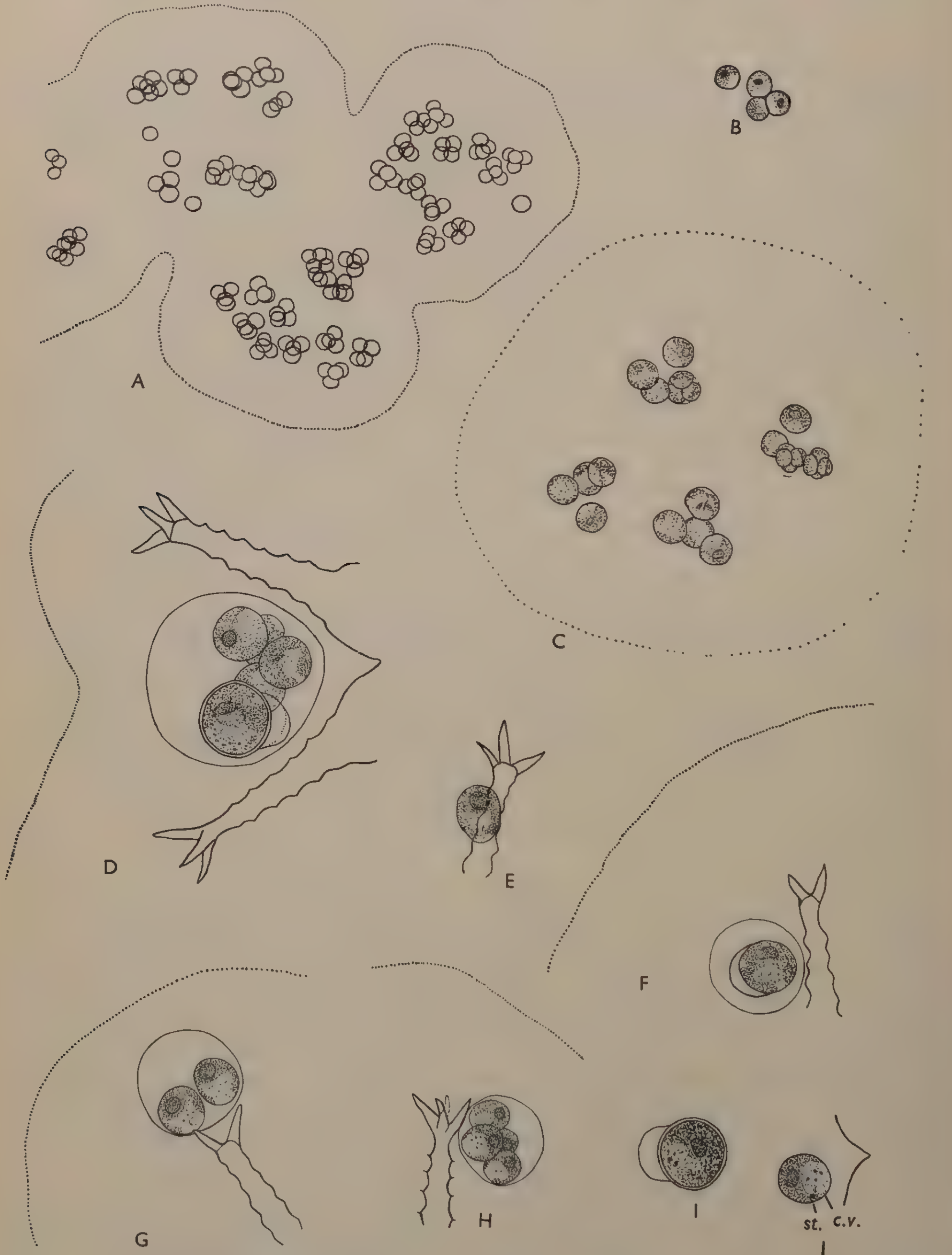

Fig. 1. A–C, *Radiococcus planktonicus* sp.nov. A, part of a large and, C, of a small colony; B, four cells. D–J, *Cecidochloris stichogloeae* Skuja. *c.v.*, contractile vacuoles; *st.*, stigma. All from living material. A, × 390; B, × 560; C, × 650. The rest × 875.

around the cells apart from pieces of the parent wall which may be faintly visible for a short while after division. The cells are characteristically arranged in tetrads (Fig. 1A), less commonly singly or in pairs. Single cells normally represent the break-up of a tetrad preparatory to cell division, while pairs are typically seen in populations growing under more or less unfavourable conditions so that only two daughter cells are produced at each division. The chromatophore is basin-shaped with a basal pyrenoid. There are no contractile vacuoles or stigma. Reproduction is solely by autospores. The alga retains its characteristic appearance when grown in solution number 10 of Chu (1942), with the addition of soil extract, though the colonies are larger and denser.

R. planktonicus is present, sometimes in abundance, in the plankton of Windermere, English Lake District and, less commonly, in that of other lakes in the same drainage basin. Type material from Windermere is lodged at the Windermere laboratory of the Freshwater Biological Association and the British Museum (Natural History), London. A culture is in the National Type Culture Collection of Algae and Protozoa, Cambridge.

In the arrangement and shape of the cells, type of chromatophore and absence of motile stages, this alga agrees with other species of *Radiococcus*. *R. nimbatus* (De Wild.) Schmidle and *R. wildemani* Schmidle differ in the presence of a radially striated mucilage envelope around the groups of cells (Schmidle, 1902). The former is epiphytic and has larger cells (8–15 μ diam.) and the latter cells (3–5 μ diam.) with a much thickened chromatophore and almost central pyrenoid. *R. pelagica* Teiling (1946, fig. 1) is also planktonic and lacks the radially striate mucilage, but differs in the globose or tetrahedral colonies, the common occurrence of botryoidal groups of eight cells (which reach 13–18 μ diam.) as well as four tetrahedrally arranged, while large fragments of the mother cell walls seem to be a prominent feature of the colony.

R. planktonicus might be confused with *Sphaerocystis schroeteri* Chod. (*Gloeococcus schroeteri* (Chod.) Lemm.), a species whose taxononic limits are still unclear, though some of the taxa included in the original description (Chodat, 1897*a*, *b*) have now been placed elsewhere (Lund, 1952; 1956). Even now it is still an aggregate species and some of the taxa included therein have small cells, while zoospores are rarely produced and in all, as in *Radiococcus*, cell divisions are not synchronous throughout the colony. Nevertheless, the characteristic random distribution of large numbers of small cells in tetrads in colonies which reach considerable size, and in so doing lose any original globose shape, make it relatively easy to distinguish *Radiococcus planktonicus* not only from *Sphaerocystis* but also from other common members of the Windermere plankton such as *Gemellicystis*, *Paulschulzia*, *Gloeocystis* and *Planktosphaeria*.

(2) **Cecidochloris stichogloeae** Skuja, 1948, p. 100 (Fig. 1D–J)

The non-motile cells (6–9 μ diam.) usually lie at a varying depth within the mucilage surrounding planktonic algae, notably desmids. They may also be attached to species lacking mucilage envelopes, such as *Asterionella formosa* Hass. or *Dinobryon divergens* Imhof. The former is by far the commoner habitat and, in British material, it has been most frequent in the mucilage of *Staurastrum anatinum* Cooke & Wills. When growing within the colonies of other palmelloid green algae, such as *Gemellicystis neglecta* Teil. em. Skuja, it may easily be mistaken for a reproductive stage.

After the zoospore has come to rest within or on the host alga, the non-motile cell is for a time identical with it, apart from the loss of the flagella and, perhaps, a more globose shape (Fig. 1E, J). Later, it produces a wide envelope which, according to Skuja (1948), arises from the original wall, a new one soon replacing it. Typically, this cell and the colony derived from it lie close to that part of the envelope nearest to the wall of a host cell, with the anterior pole facing inwards and the posterior one outwards (Fig. 1D, F–H). The cell enlarges somewhat and becomes globose before division to form four or, less commonly, two identical daughter cells. Whether the latter are originally flagellate or not, that is are zoospores, is not known, though the absence of any trace of flagella in the smallest cells observed suggests that they are aplanospores. These daughter cells may repeat the process so that the largest colonies observed consist of sixteen cells, each quartet within its own envelope. Alternatively, zoospores are formed and escape from the host. These are biflagellate, ellipsoid to ovoid or, rarely, almost globose. They were so rarely observed in the British material that no detailed examination was possible. Encysted cells (11–13 μ diam.) are sometimes produced. The parent wall breaks on one side, but the other part remains attached to the larger cyst so that the relationship resembles a globose acorn in its cupule (Fig. 1D, F, I). Attempts at germinating these resting cells failed.

The young non-motile cell retains the two anterior contractile vacuoles and the small discoid stigma of the zoospore, together with the basin-shaped chromatophore and basal pyrenoid (Fig. 1E, H, J). Both contractile vacuoles and stigma are lost in the mature cell and the chromatophore becomes massive, so much so in the resting cells that its original shape is more or less lost.

Cecidochloris is most frequent in Windermere, but is also present in other lakes in the English Lake District and Ireland. Its mode of occurrence in Britain contrasts markedly with Skuja's (1948) description of Swedish material which made the name appear to be so apt. Skuja found it mainly in the outer layer of the mucilage of *Stichogloea doederleinii* (Schmidle) Wille. There, the zoospore settles on the surface, which is dissolved over a small area around it. The non-motile stage, which is then produced, looks like a gall. No sign of any solution of the mucilage of the British host plants could be detected, though the zoospores often penetrate deeply within their envelopes (Fig. 1D, F–H). The encysted stage was not seen in Sweden.

(3) **Elakatothrix gelatinosa** Wille var. **aplanospora** var.nov. (Fig. 2)

The cells (12–36 μ length; 3–4 μ breadth) agree closely with those of var. *gelatinosa* (e.g. Wille, 1898; Smith, 1920; Skuja, 1948), though their length may be greater. The colonies (to 260 μ length; 170 μ breadth) and the arrangement of the cells within them, however, may appear very different from those typical of var. *gelatinosa*. The colonies are often very broad and of irregular shape (Fig. 2D, G), but small ones (Fig. 2B, F) may have the ellipsoid, fusiform or cylindrical shape characteristic of var. *gelatinosa*. In large colonies, up to eighty cells may be present and are more or less irregularly arranged (Fig. 2D, G), though the linear arrangement characteristic of var. *gelatinosa* may not be entirely absent. There is a strong resemblance to *Quadrigula lacustris* (Chod.) Smith and *Q. Chodati* (Tanner-Fullm.) Smith[1] (Smith 1920). Nevertheless, the cells multiply by transverse division (Fig. 2B, C, N, O), and no autospores are formed. The chromatophore is similar to that of var. *gelatinosa*, apart from the occasional presence of two pyrenoids (Fig. 2H, K, L) or, very rarely, even two chromatophores (Fig. 2J), both stages possibly being a prelude to cell division, for both have divided by an early stage in this (Fig. 2C, N). Cells with two pyrenoids are indistinguishable from those of *Quadrigula chodati*, since they lie one to each side of a central depression in the chromatophore (Fig. 2K, L). The cells of *Elakatothrix viridis* (Lemm.) Printz often have two pyrenoids, but they are of different shape.

The differences noted above scarcely justify separating this alga from the type, but in the formation of aplanospores it is unique in the genus. These generally arise in the large colonies of irregular shape (Fig. 2D, E, G, but see also F). Any cell may produce a spore, but all the cells rarely do so (Fig. 2D–G). The protoplast contracts into an oval to ellipsoid mass in the centre of the cell whose wall is often inflated there in consequence (Fig. 2P). At the same time two contractile vacuoles are formed. The inflation represents

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[1] Both these species are perhaps better placed in *Ankistrodesmus* (see Bourrelly, 1951).

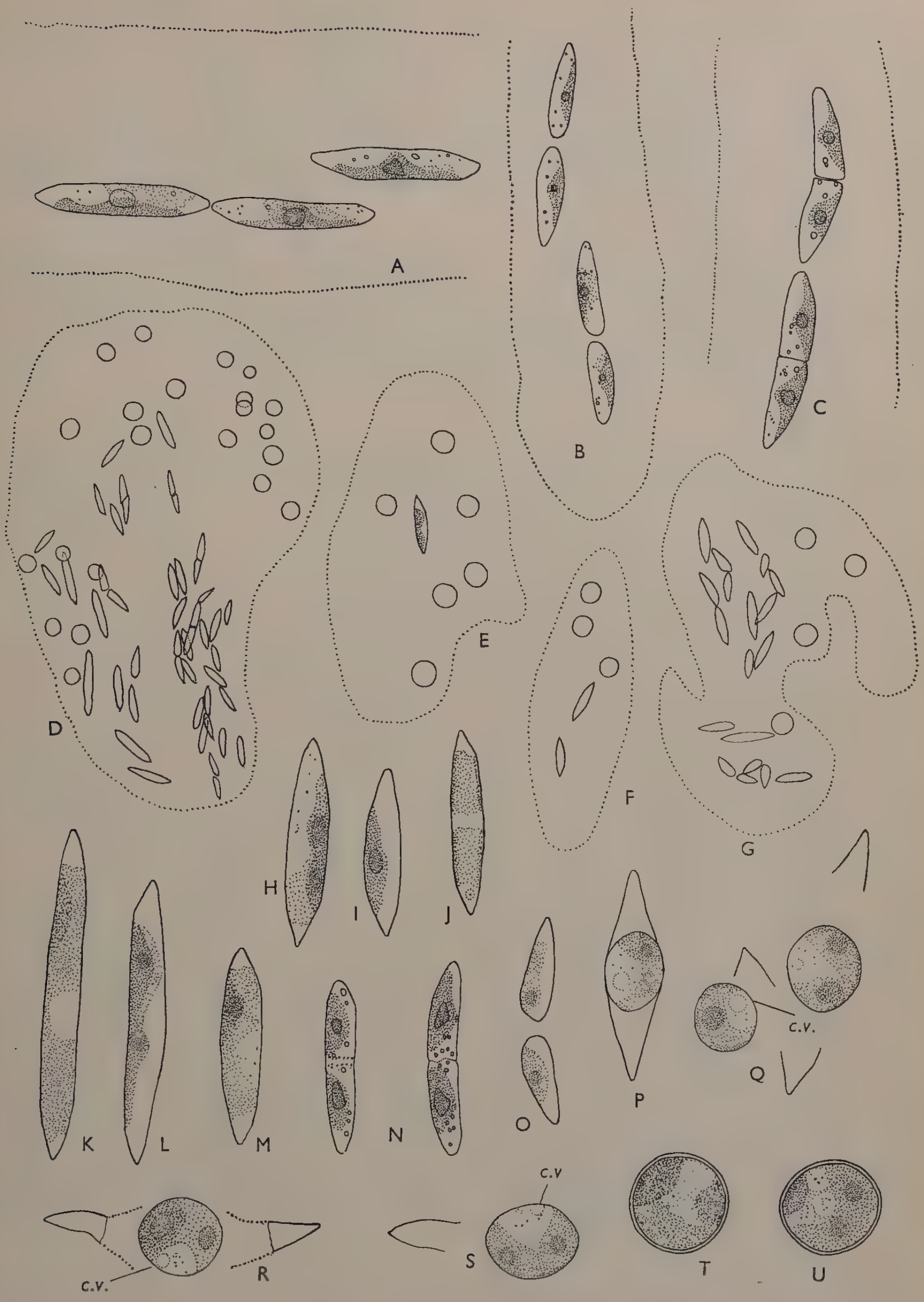

Fig. 2. *Elakatothrix gelatinosa* Wille var. *aplanospora* var.nov. A–C, cells from elongate colonies; D–G, colonies of varied shape and size with aplanospores; H–M, range of cell size and chromatophore structure; N–O, stages in cell division; P–U, aplanospores. *c.v.*, contractile vacuoles. All from living material. A–C, N–O, ×780; D–G, ×300; the rest, ×1250.

the first stage in the gelatinization of the wall around and to some distance from the contracted protoplast. Eventually, one part of the wall around the spore becomes so delicate or watery that the protoplast may be liberated (Fig. 2Q, R). In all cases, the polar regions of the wall remain unaltered so that, in the absence of staining or mounting in Indian ink, it appears as though liberation were due to a break in it (Fig. 2Q). Since the degree of destruction of the wall is related to its proximity to the developing spore, it seems clear that, in early stages, enzymes pass out of it into the empty cell cavity. After a time, the spore becomes globose, produces a relatively thick wall and loses its contractile vacuoles, reaching up to 11 μ diameter (Fig. 2T, U). Attempts to germinate the spores failed.

This alga is present occasionally in most years in small numbers in Blelham Tarn, English Lake District, and has been observed in May 1955 in the nearby Esthwaite Water by Dr H. M. Canter (Mrs J. W. G. Lund). Material is lodged in the Windermere laboratory of the Freshwater Biological Association and the British Museum (Natural History), London. Production of aplanospores usually heralds its disappearance from the plankton.

Since contractile vacuoles are present, the aplanosporic nature of the monospores can scarcely be doubted, though the formation of but one from the whole content of a cell is unusual and the possibility cannot be ruled out that this is a stage in the life-history of the species which has been overlooked. West & West (1909, Fig. 6A–D) observed colonies of rather irregular shape reminiscent of Fig. 2D, E, G.

The systematic position of *Elakatothrix* still remains uncertain, though it can no longer be placed in Printz's (1927) Pleurococcaceae. There is some resemblance to members of the Ulotrichales such as *Geminella* Turp. and *Gloeotila* Kütz., where the filaments may be short and the cells more or less widely spaced from one another, the whole plant being surrounded by a wide mucilage envelope; indeed, *Geminella monospora* Lund (1956) also produces monospores though these lack contractile vacuoles. Equally, there are members of the Chlorococcales with similar types of colonial structure whose cells divide by such oblique walls that the plane is almost transverse, the autospores reaching the adult size and shape by elongation of the new pole. Examples are *Ankistrodesmus falcatus* (Corda) Ralfs var. *spirilliformis* G. S. West and *A. acicularis* (A.Br.) var. *heteropolis* Skuja. In the latter, the new half of the cell remains shorter than the old one. Further, there are members of both the Chlorococcales and Heterococcales which produce linear rows of new cells from transverse division of the mother protoplast, so that they are scarcely distinct from filamentous genera. A notable example is the ?*Bumilleria* of Lund (1947, p. 53), which is actually a species of the coccoid genus *Bumilleriopsis* Printz (1914, p. 50), in which threads of considerable length may be produced (cf. *B. filiformis* Vischer, etc., in Vischer, 1936, 1945; Pascher, 1937–9). The fundamental distinction between a coccoid and a filamentous structure would appear to rest on the fate of the middle lamella of the parent cell. If this is continuous with that of the daughter cells, though they later separate, then the alga is presumably filamentous. A cytological study of *Elakatothrix* and other algae of similar uncertain affinity is needed. For the present, it appears to me that the structure of the large colonies at least points to *Elakatothrix* being a coccoid alga. The word coccoid is here used in a broad sense to cover also palmelloid forms, since, in my view, there is no fundamental distinction between most of these algae and those generally classed in the Chlorococcales.

(4) **Gemellicystis neglecta** Teiling, 1946, p. 67, em. Skuja, 1948, p. 110 (? *Tetraspora lacustris* Lemm. p.p. 1898, 1899? *Sphaerocystis Schroeteri* Chod. p.p. 1897*a*, *b*), Fig. 3

The colonies (to 200 μ length; 60 μ breadth) may be somewhat flattened, though they usually appear oblong, oval, widely elliptical or, very rarely, almost spherical in shape no matter whether they are viewed from one of the broader or narrower sides. There are up

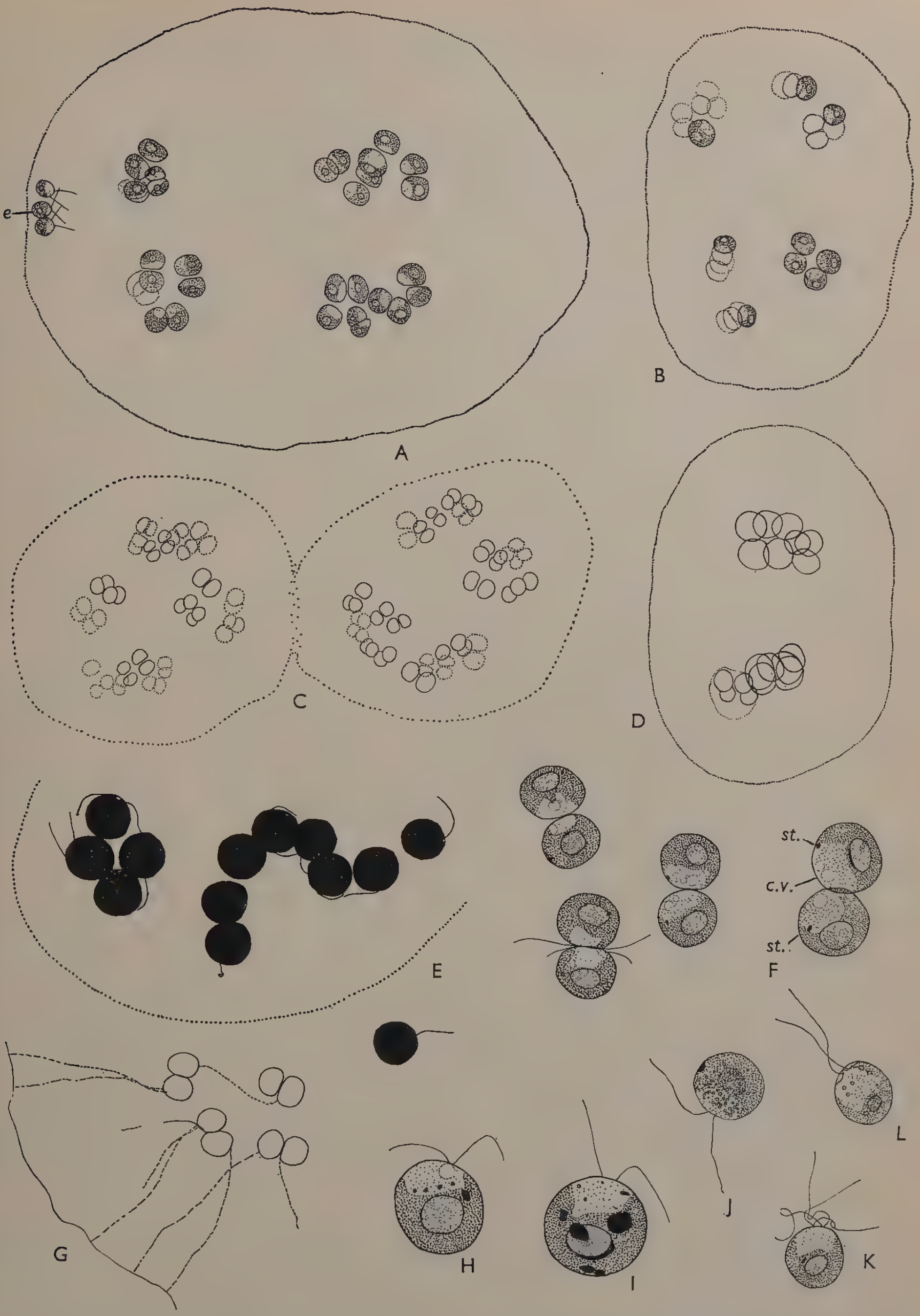

Fig. 3. *Gemellicystis neglecta* Teil. em Skuja. A, C, two colonies from the broader: and B, D, two from the narrower sides; E, part of a colony with bi- and uniflagellate cells, one of which has escaped (bottom right); F, cells with stigmata and contractile vacuoles; G, part of a colony showing apparent pseudocilia; H–L, swarmers. *c.v.*, contractile vacuoles; *e*, *Chlamydomonas epiphytica st.*, stigma. E, G–I, stained in iodine in potassium iodide; J–L, killed in 1 per cent osmic acid; the rest from living material. A, B, D, × 340; C, × 220; E, F, left-hand group of six cells, × 800; right-hand two cells, × 1100; G, × 550; H, I, × 1250; J–L, × 850.

to 150 cells, but the great majority of colonies have from eight to sixty-four. The cells are in quadrate, cruciate or cubic quartets or in pairs, while a few may be solitary; they are never in tetrads nor botryoidal groups. The groups of cells may be close together, or more or less widely apart; a common arrangement is for the cell groups, as a whole, to occupy two parts of a colony, the central zone being empty (Fig. 3A–D). The mucilage is homogeneous and the groups of cells do not lie within any visible separate envelopes except during or very shortly after division (Fig. 3D, left-hand bottom quartet of cells). The mucilage contracts in formalin, and this presumably explains Teiling's (1946) fig. 2. The colonies may fragment by an approximately median 'fission'. The mucilage contracts and apparently becomes more diffluent around the central zone lacking cells until two portions of more or less equal size separate (Fig. 3C, and Skuja, 1948, Taf. XI, figs. 10–12).

The cells (8–14 μ length; 7–10 μ breadth) vary in shape according to the rate of multiplication. Usually, each quartet consists of two pairs lying in the same or higher and lower horizontal planes (Fig. 3A–C). In each pair, the cells are close together, often in contact along part of their apical margins which are somewhat flattened (Fig. 3A, C, F). This arrangement, together with the irregular spatial distribution of the cell groups within the colony, gives the alga a very distinctive appearance even in the presence of the other palmelloid algae which commonly accompany it (e.g. *Gloeocystis*, *Sphaerocystis*, *Radiococcus*, Fig. 1A). The cells are normally seen under the microscope from their broad sides because these lie in the plane of greatest width of the colony. If, however, a colony is viewed from one of the narrower sides, this characteristic appearance is lost (Fig. 3D). If multiplication is proceeding fast enough, most of the cells will be arranged as described above, though they become more globose as division approaches. In old or slow-growing material most of the cells are globose, as may also be the case preparatory to the assumption of motility (Fig. 3E). Shortly after division the daughter cells can be seen within a globose envelope formed from the enlarged parent wall (Fig. 3D). There are two apical contractile vacuoles and a small or minute stigma commonly, though not always, located in the anterior half of the cell (Fig. 3F). According to Skuja (1948) this is absent (1948, p. 112), or usually so (1948, p. 110), but in the British material the opposite is the case, though it is easily overlooked. The wall is thin and devoid of a papilla. The parietal chromatophore is basin-shaped with a massive basal thickening containing the pyrenoid which is usually elliptical, oblong or oval and rarely globose (Fig. 3A, B, F). In the Swedish material Skuja (1948) finds the chromatophore to be often more or less markedly dissected longitudinally so that it has a ribbed appearance, but this has never been seen in British specimens. Not uncommonly, some or all the cells have two immobile flagella (Fig. 3F), which were originally thought to be pseudocilia (Teiling, 1946). I can support Skuja's (1948) view that these structures are all true flagella, for I have often seen cells with originally motionless flagella begin to move them and finally to swim away. Sometimes in colonies in Lugol's solution one or two lines of stained material pass from the cell to the periphery of the colony, so simulating pseudocilia (Fig. 3G); no other stain produces such an effect. Transformation of vegetative cells into swarmers of identical size, shape and structure is not uncommon (Fig. 3J). In addition, cell division may be followed almost at once by the assumption of motility, so that these zoospores may not be as large or globose as adult vegetative cells. Rarely, motile cells have a plasma papilla (Fig. 3L, see also Skuja, 1948, Taf. XI, fig. 21), which may easily be mistaken for a wall papilla owing to the delicacy of the membrane. The flagella are about as long as the cell is wide or up to twice as long. In material from Coniston Water and Windermere, some cells produced only one flagellum (Fig. 3E), but swam freely, if in an irregular manner, while, very rarely, cells with two pairs of flagella were seen (Fig. 3K).

Gemellicystis neglecta is a common and sometimes abundant plankton alga in those British lakes which are neither very strongly eu- nor oligotrophic. Thus it is present in all the lakes in the English Lake District except Wastwater, Buttermere, Ennerdale and Brothers Water, common in Scotland, rare in the more calcareous Irish lakes and those of central and eastern England (absent in the Norfolk Broads). It may be infected, in lakes in the English Lake District, by three chytridiaceous parasites (Canter, 1950, 1951, 1953, 1954), sometimes severely. Dr A. J. Brook (in litt.) informs me that in Loch Kinardochy, Perthshire, an abundant growth of this alga was very largely destroyed by such a fungal epidemic. Unidentified Protozoa may also ingest numerous cells. The mucilage harbours few epiphytes apart from *Chlamydomonas epiphytica* G.M. Smith (Fig. 3 A, e), *C. gloeophila* Skuja and *Cecidochloris stichogloeae* Skuja. In the English Lake District, numbers are low in winter and reach a maximum in mid- and late summer. It is probably widespread throughout the Northern Hemisphere.

It is probable that many British records of species of *Tetraspora*, *Sphaerocystis* and *Gloeocystis* are really of *Gemellicystis*. The cause of these misidentifications can be found in its nomenclatural and taxonomic history, which was first elucidated by Teiling (1946). In 1898 Lemmermann described, and in 1899 figured, as *Tetraspora lacustris* Lemm. an alga which I agree with Teiling (1946) is indistinguishable from *Gemellicystis*. It is hard to understand why Lemmermann was then unaware that pseudocilia were present, though he neither mentions nor figures them, since he must have known that *Tetraspora* is characterized by their presence. The exact identification of his alga of 1898 and 1899 must therefore remain uncertain; it may be that he confused these two alga whose cells may be of more or less similar size and shape. In 1897 (*a*, *b*) Chodat described and figured *Sphaerocystis schroeteri* Chod. (*Gloeococcus schroeteri* (Chod.) Lemm. of some authors—see Lund (1956)) which is easily distinguished from *Gemellicystis* by the tetrahedral or botryoidal groups of cells within a usually more or less globose envelope,[1] and from *Tetraspora* and *Paulschulzia* (see p. 608) by the absence of pseudocilia. Chodat (1902) himself added to the confusion by suggesting that *Tetraspora lacustris* was a stage in the life history of *Sphaerocystis schroeteri* (cf. G. S. West, 1904, p. 242). There can be no doubt that only a part of Chodat's (1897 *a*, *b*) original description and figures refer to *Sphaerocystis schroeteri* as now generally understood by algologists. Though he included at least three different algae in his general description (see Lund, 1952), apart possibly from pl. 9, fig. 12 (Chodat, 1897 *b*; see also Teiling, 1946), none of these resembles *Gemellicystis*. In 1915 Lemmermann (in Lemmermann, Brunnthaler and Pascher) first mentioned the presence of pseudocilia in *Tetraspora lacustris*, though there was still no description of the cell contents. Chodat never included this alga of Lemmermann's in *Sphaerocystis*, though some later references (e.g. West & Fritsch, 1927) give the impression that he did. Lastly, Teiling's (1946) misinterpretation of the flagella as pseudocilia temporarily revived an apparent relationship between the two algae, although he clearly showed that there were other differences between them. Skuja (1948) made it clear that, in the alga he believed to be identical with Teiling's *Gemellicystis*, pseudocilia were absent but added that, should it turn out that the *Gemellicystis* of Teiling really has pseudocilia, then his *Gemellicystis* must be removed to a different genus for which he proposed the name *Planktogloea*. There is no doubt in my mind that Teiling's (1946), Skuja's (1948) and the *Gemellicystis* here described are all one and the same and lack pseudocilia.

(5) **Paulschulzia pseudovolvox** (Schulz) Skuja, p. 118 (*Schulziella pseudovolvox* (Schulz) Teiling, *Tetraspora pseudovolvox*) Schulz (Figs. 4–6)

The British specimens are described first, and comparisons between them and Swedish and Finnish material later. The relationship between *Tetraspora* and *Paulschulzia* is considered on p. 610.

The globose to broadly ellipsoid colonies (40–350 μ, usually less than 200 μ diam.) commonly contain from four to sixty-four cells, two being the least and 248 (Fig. 6 E) the

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[1] Nevertheless, these two algae are still confused, even in material from lakes from which Chodat (1902) recorded his alga; for example, the *Sphaerocystis schroeteri* in Jaag & Nipkow (1950) is *Gemellicystis neglecta*.

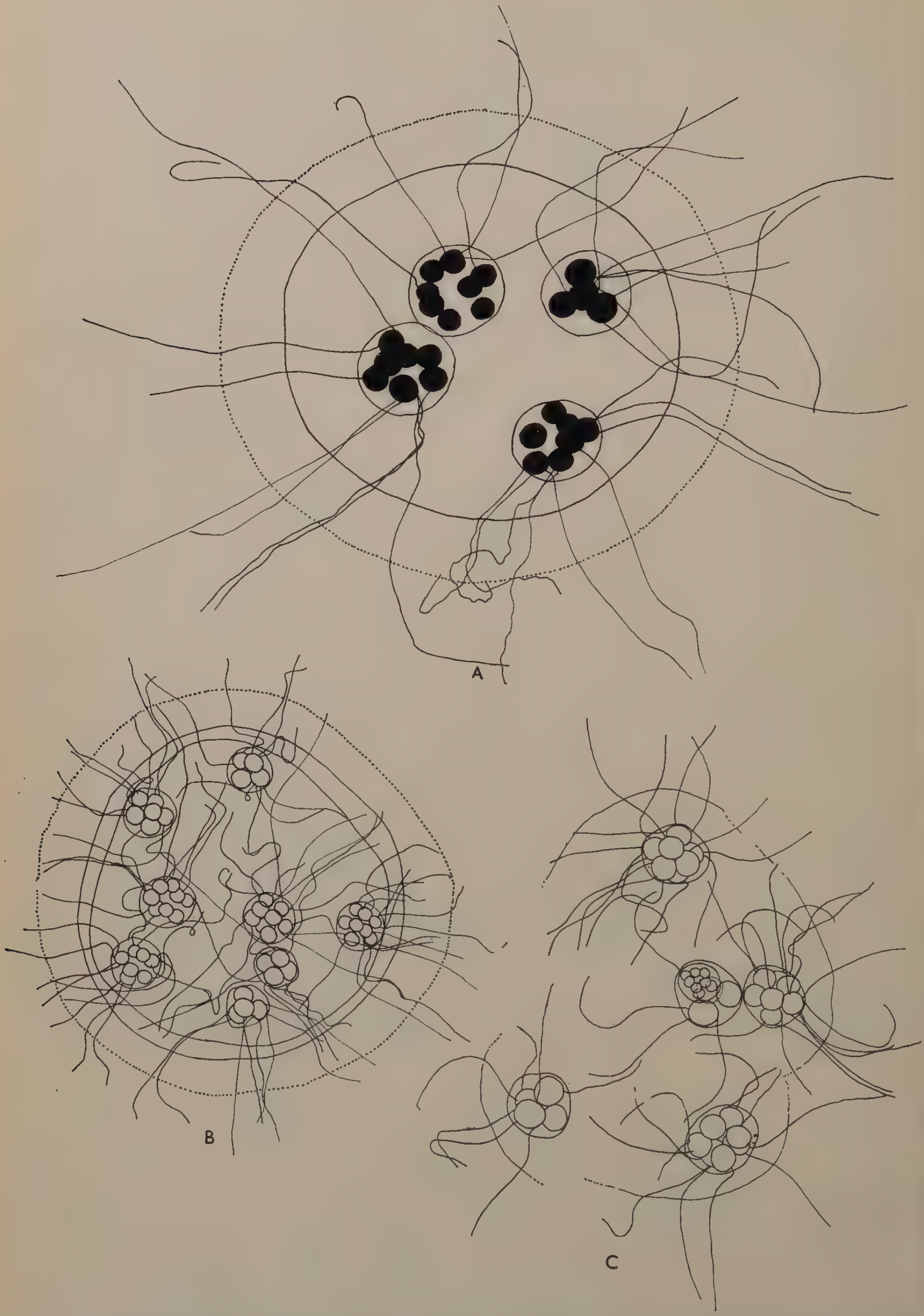

Fig. 4. *Paulschulzia pseudovolvox* (Teil.) Skuja. A–C, colonies; in C, three of the daughter colonies have been liberated from the disintegrating parent colony; in none are all the pseudocilia depicted. A, stained in 1 per cent alkaline gentian violet in aniline water. A, ×450; B, C, ×200.

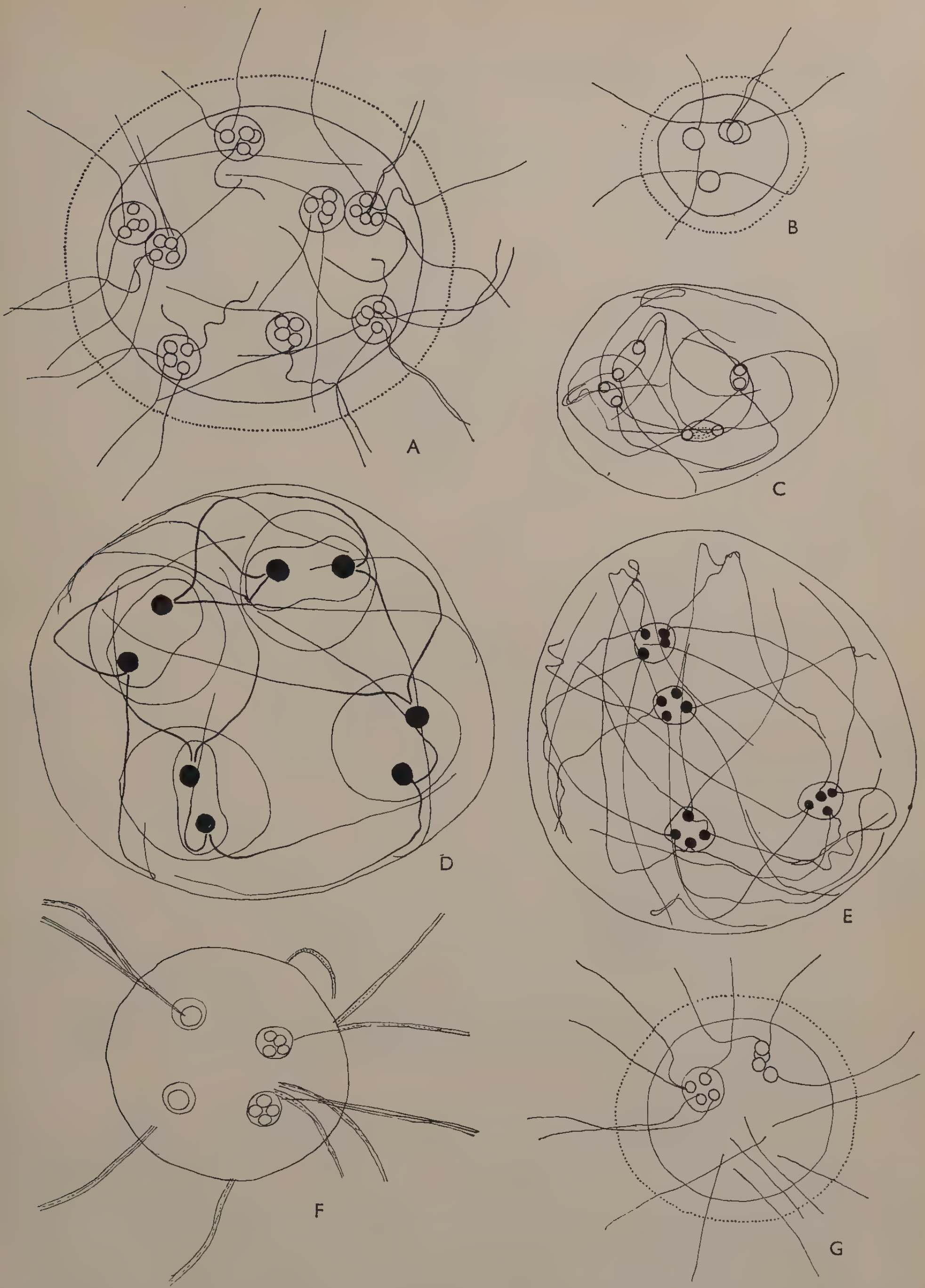

Fig. 5. *Paulschulzia pseudovolvox* (Teil.) Skuja. A, colony with four-celled daughter colonies; and B, with only four cells (equivalent to one daughter colony of A); C–E, colonies with pseudocilia extending beyond envelopes of daughter but not of parent colony; F, parts of pseudocilia outside the colonial envelope as seen in an indian ink mount; G, colony some of whose cells have become motile. C–E, stained in 1 per cent alkaline gentian violet in aniline water; the rest from living material, G under phase contrast. A–C, E, G, ×200; D, ×300, F, ×450.

largest numbers observed. The cells are in a single group, or up to sixteen such groups, each within a clearly visible, separate envelope. The whole colony is bounded by a firm layer of mucilage which is also clearly visible, and itself normally lies within a more delicate outermost layer (10–25 μ thick), which may or may not be visible without staining or mounting in indian ink, and which disappears before the liberation of the daughter colonies (Figs. 4 A–C; 5 A, B). The cells are in tetrahedral or botryoidal groups, but as the colonies enlarge they may become more or less widely separated (e.g. Figs. 4A; 5A; 6E). This, however, depends partly on the rate of multiplication; if this is rapid, separation may not take place (Fig. 4C). Division is usually into four or eight cells (Figs. 4; 5A, E), but there may be only two (Fig. 5C, D) or sixteen (Fig. 6C, E) daughter cells. Though these are normally aplanospores, they can function as zoospores. All the cells in a colony generally divide at approximately the same time, but when they do not (Figs. 4B; 6C, one daughter cell or colony in each case) there is a superficial resemblance to *Sphaerocystis*, if the pseudocilia are not noticed. The cells do not necessarily all produce the same number of daughter cells (Fig. 4A–C, with daughter colonies containing four, and sixteen cells). The daughter colonies are liberated by disintegration of the colonial envelope and very rarely one or more grand-daughter colonies may already have been produced (Fig. 4C). The size of the cells when reproduction starts is also variable (daughter colonies with two or four cells and pseudocilia enclosed within the colonial envelope are described later). The colony is, then, generally composed of three generations; the common bounding membrane being derived from the first, the envelopes to the daughter colonies from the second and the cells themselves from the third, but in a plant with grand-daughter colonies (Fig. 4C) a fourth generation is represented.

The globose cells (6–13 μ diam.) have a delicate wall without a papilla. Each bears two long pseudocilia (to 200 μ length; usually about 75–100 μ) which generally project beyond the outermost investment to the colony (Figs. 4A–C; 5A, B, F, G). In some colonies, though they extend far beyond the envelopes of the daughter colonies, they lie within that enclosing the whole colony. As their length is no less than usual, they follow a contorted course, the more distal portions often lying close to the colonial envelope (Fig. 5C–E). Such colonies consist of small numbers of cells, for there are rarely more than four daughter colonies each with two to four cells. These daughter colonies may also be peculiar in possessing two envelopes (Fig. 5D), while the cells are pale in colour and more widely spaced apart than usual. The pseudocilia of all colonies may, or may not, be wholly visible without staining or observing under phase contrast, but a part at least is generally obvious. When stained, they may be clearly broader in the basal than in the more distal portions (Fig. 5D). In colonies immersed in diluted indian ink they are seen to be relatively thick, at least in the portions outside the colonial envelope (Fig. 5F). There is a thicker outer homogeneous sheath and a narrow inner one which is somewhat granular and is presumably the protoplasmic thread as in *Tetraspora* (Fritsch, 1935, p. 122).

The protoplast may have a plasma papilla (Fig. 6D) which, owing to the delicacy of the wall, may be mistaken for a wall papilla. There is a basin-shaped chromatophore with a pyrenoid in the more or less thickened basal region (Fig. 6A–D). There are two apical contractile vacuoles and, in the cells of some colonies, a stigma, but this may be a preliminary to the assumption of motility. Any vegetative cell may become motile by the production of two flagella and loss of the pseudocilia (Fig. 5G). Thus, the swarmers are of similar structure, apart from the rod-shaped stigma, but their size and shape are variable (Fig. 6, and compare Skuja, 1948, Taf. XIV, figs. 10–14). Under laboratory conditions, motility does not last more than a few hours. On coming to rest, the swarmer becomes globose and soon produces a wide mucilage envelope; sometimes it already possesses one (Fig. 6K). Division follows to form a new colony.

Paulschulzia pseudovolvox has been collected in a very small, shallow, non-calcareous, nameless tarn near Little Asby, Westmorland (Ordnance Survey grid reference 675078), during the last few summers. It is also present in small numbers in the nearby calcareous Sunbiggin Tarn. It may be in the plankton, but seems to be more common in macrophytes and on the deposits, though, in the small tarn, the water is so shallow that the various communities are scarcely separate.

P. pseudovolvox grows well in liquid culture (medium no. 10 of Chu, 1942, with soil extract) and maintains its characteristic form if regularly subcultured and shaken occasionally. It can also be grown on agar when the characteristic colonial form is lost;

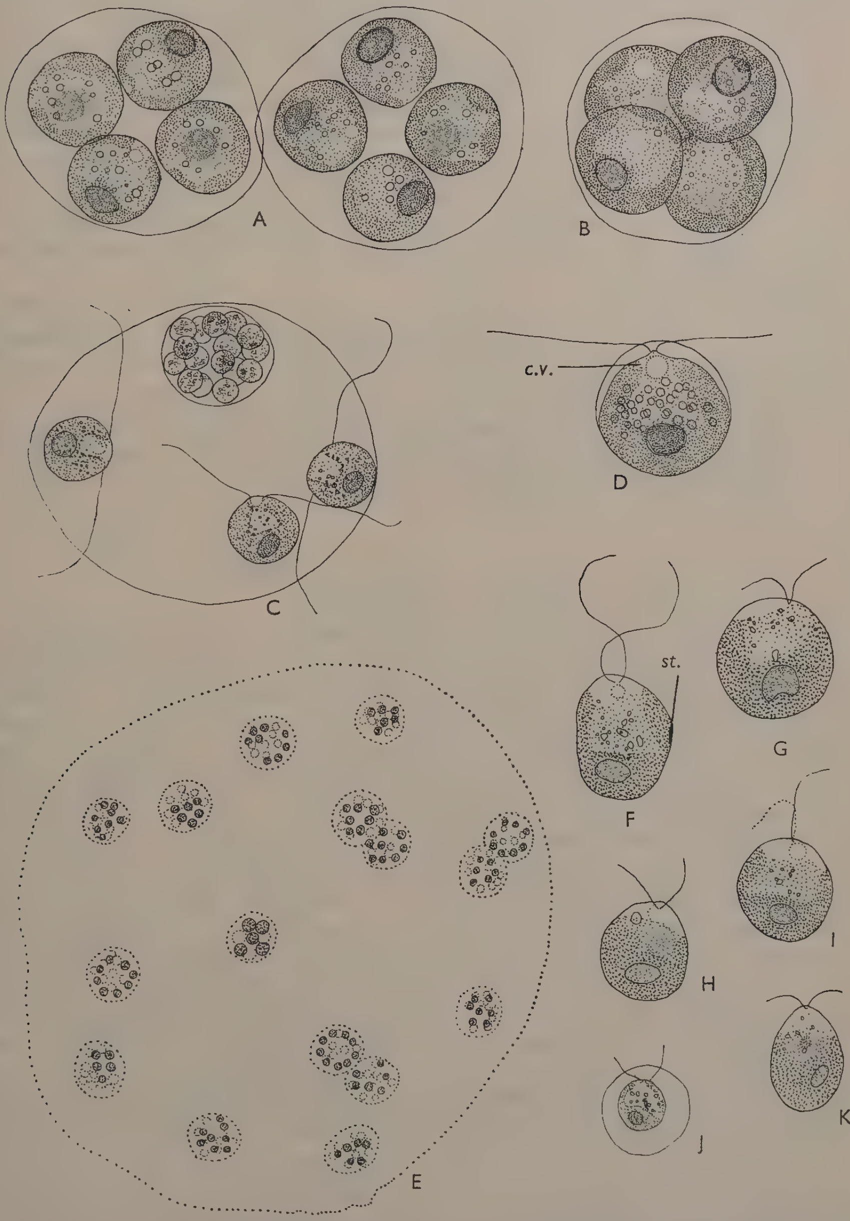

Fig. 6. *Paulschulzia pseudovolvox* Teil. em. Skuja. A–D, cell structure, parts of pseudocilia shown in C and D, the latter with plasma papilla; E, largest observed colony, pseudocilia not depicted; F–K, swarmers. F–K, killed in 1 per cent osmic acid, the rest from living material. *c.v.*, contractile vacuole; *st.*, stigma. A, B, D, F–I, K, ×1250; C, ×1100; E, ×125; J, ×660.

this may also be the case in dense liquid cultures which are not shaken, for then the daughter colonies cannot separate from one another.

The Swedish specimens described by Skuja (1948, p. 118) differ in the normally somewhat rostrate apex to the cell, while the chromatophore may have a number of arms radiating upwards and outwards from the basal pyrenoid. The colonies and pseudocilia, too, are generally smaller but size is very much a reflexion of environmental conditions. The Swedish specimens described by Teiling (1942) all contained sixteen or less cells and the pseudocilia never projected beyond the colonial envelope, indeed not necessarily from that surrounding the daughter colonies either (Teiling, 1942, figs. 1 and 5). Skuja (1948) considers this to be an artifact induced by fixation and staining, but the presence of similar colonies (Fig. 5C–E) in fresh British material, in company with normal ones, shows that Teiling's description, in so far as it refers to this species, is correct. In both cases, the colonies contained few cells. In cultures, such colonies commonly appear when the population is near its maximum density, and Teiling's material may well have been collected when the environmental conditions were more or less unfavourable (see also Schulz's, 1923, figures). However, it is not certain that all his material belongs here, for figs. 1 and 5 (Teiling, 1942) would appear to belong to *P. elegans* (Woron.) Lund for the reasons given on p. 608.

Teiling (1942) rightly points out that the *Tetraspora lacustris* of Nygaard (1945) is not the same as Lemmermann's alga (see Lemmermann, 1915, fig. 21; and the discussion here under *Gemellicystis neglecta*, p. 601). Tentatively, he made this a new species *T. nygaardii*, but the colony structure appears to be that of a *Paulschulzia* and, as it is not clear to me that it is distinct from *P. pseudovolvox*, its position is best left uncertain; similarly, *Tetraspora lamellosa* Prescott (see Prescott, 1951, pl. 5, fig. 6) may also belong to this genus, though Ettl (1955) places it in his *Fottiella* as *F. lamellosa* (Presc.).

(6) **Paulschulzia elegans** (Woron.) comb.nov. (*Tetraspora elegans* Woronichin, 1949, p. 34) (Figs. 7–9)

The globose to widely ellipsoid colonies (to 200 μ diam. or length) contain two to eight cells or daughter colonies within a mucilage envelope which, as in the previous species, may consist of two layers (e.g. Fig. 9), the outer usually less than 10 μ in thickness. The cells (to 15 μ diam.) lie approximately equidistant from one another, their separation arising early in the development of the daughter colony (Fig. 8A, B, D, E). They are globose with two anterior contractile vacuoles, a basically parietal basin-shaped chromatophore, though this may be somewhat irregular in outline due to lobing, and a basal pyrenoid (Fig. 8G–I). There is neither a stigma nor a papilla to the wall though, rarely, there is a plasma papilla if the protoplast lies some distance within the wall. Each cell has two long pseudocilia (to 190 μ length) lying within the colonial envelope or, when daughter colonies are present, within their envelopes (Figs. 7, 8). Occasionally, the pseudocilia are more or less markedly split as in *Tetraspora hexanematoidea* (Lund, 1956), and these are presumably the origin of the accessory one or two pseudocilia which are sometimes present (Fig. 7E, G). The pseudocilia may run for a considerable distance just within the colonial envelope. Occasionally, in stained material or that which has been preserved in formalin, a small part of a pseudocilium projects beyond the mucilage envelope (Fig. 7F, H, cf. Teiling, 1942, fig. 1, of *Schulziella pseudovolvox*), but this has never been seen in live material. If, however, living colonies are placed in agents which contract the mucilage, such as may be the case with 1 per cent methylene blue or gentian violet, one or more pseudocilia may be seen to pass through the contracting envelope. Further, replacement of the stain by water commonly leads to a complete reversal of the process, though sometimes a small portion may fail to be recovered. It seems, therefore, that the occasional small projecting portions of one or more pseudocilia in formalin material arise in the same way. The pseudocilia have small globose to ellipsoid inflated

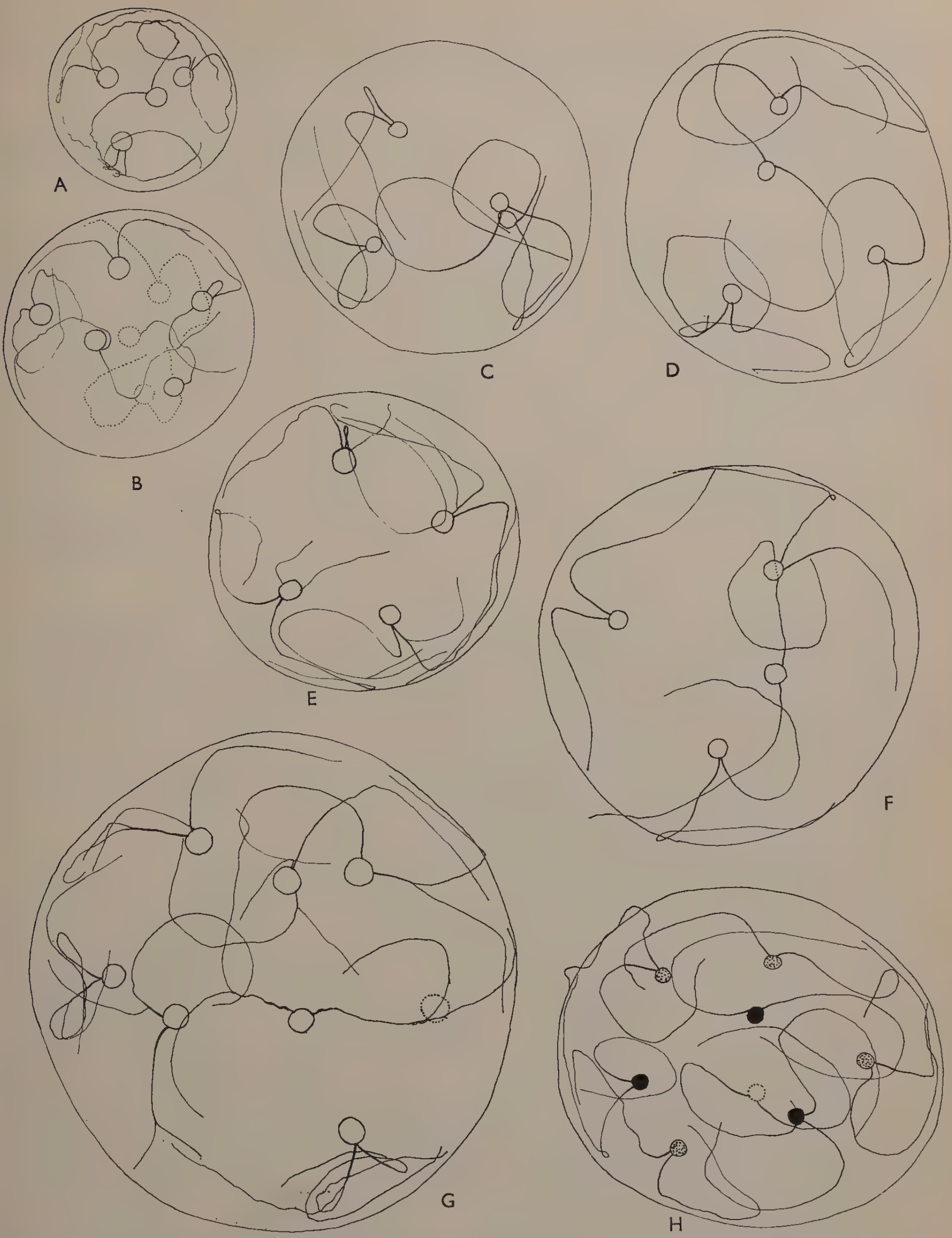

Fig. 7. *Paulschulzia elegans* (Woron.) comb.nov. A–C, typical four-celled colonies from Windermere, D–G from Bassenthwaite Lake, and H from Windermere. All from material in formalin and × 270.

portions distributed at random along their length (Fig. 8F) and their basal portions can often be seen to be broader than the rest (Figs. 7E, G; 8A) (fig. 5 of Teiling's, 1942, *S. pseudovolvox*). In reproduction, the pseudocilia of the mother cells are cast off and can sometimes be seen attached to the outside of the envelopes of the young daughter colonies (Fig. 8A). When two layers are present in the colonial envelope they disappear at maturity. The young colonies have a well-defined outer layer (Fig. 9A, B) which becomes more and more diffuse as they develop (Fig. 9B–E). The new outer membrane of the daughter colonies arises shortly after or even before they are liberated from the parent (Fig. 9D–G).

No other method of reproduction is known. Despite plentiful material from various lakes and cultivation in the laboratory for more than two years, no motile cells have ever appeared.[1]

Paulschulzia elegans is present in several lakes in the English Lake District, notably Windermere and Bassenthwaite. It is probable that the *Tetraspora lacustris* Lemm. of the Wests (1909), Pearsall & Pearsall (1925), and Pearsall (1932) is, in part at least, this species. Woronichin (1949) found a few specimens in the River Boljšaja Nevka, near Leningrad, none of which contained any daughter colonies, nor could he determine the nature of the chromatophore. I have observed algae which either belong to this species or closely related taxa in lakes in Scotland and Ireland. It is, however, not yet clear as to how variable this species is, so that other algae which at present appear to be distinct may not be so. There are also algae similar in colonial and cellular structure which differ in that the pseudocilia project from the mucilage envelope as in *Paulschulzia pseudovolvox*, to which species they may well belong. The populations of *P. elegans* in Bassenthwaite and Windermere are identical in structure but differ in size. In general, those in Bassenthwaite are the larger, and the cells are correspondingly farther apart (compare Fig. 7A–C with D–E, and G with H; Fig. 8A and D with B and E).

The reasons for transferring Woronichin's (1949) species to this genus will be clear from the discussion below of the differences between the two genera. That the British material is identical with the Russian is certain from Woronichin's account and figure (1949, fig. 1).

P. elegans grows well in solution no. 10 of Chu (1942), provided soil extract is added. Pseudocilia are then usually absent or short (Fig. 8I), but even when they are well developed they still remain within the colonial envelope. Despite numerous variations in the type and strength of culture solution used and in the physical conditions, no method has been found of preserving in culture the regular production of the long and characteristic curved and twisted pseudocilia of natural populations.

P. elegans differs most markedly from *P. pseudovolvox* in the retention of the pseudocilia within the colonial envelope. Those specimens of *P. pseudovolvox* (Fig. 5C–E) in which the pseudocilia of the daughter colonies do not penetrate the parent envelope show some resemblance to those of *P. elegans*, particularly since they are also usually of similar size. However, in the latter, the pseudocilia never pass beyond the confines of the daughter colony (compare Fig. 5C–E with Figs. 7 and 8). Colonies of *P. pseudovolvox* are generally larger than those of *P. elegans*, and the daughter colonies are retained for a prolonged period instead of being soon liberated, indeed, even grand-daughter colonies may arise before dissolution of the colonial membrane (Fig. 4C), a state unknown in *P. elegans*. *P. pseudovolvox* often produces several daughter colonies with eight cells and, especially in culture, of sixteen cells (Fig. 6E). *P. elegans*, even under the best cultural conditions, does not produce sixteen-celled daughter colonies. The cells of *P. pseudovolvox* normally remain close together, while those of *P. elegans* are spaced widely apart. In an experiment in solution no. 10 of Chu (1942) with soil extract, when the two species were grown under identical conditions (continuous illumination by 80 W. daylight fluorescent lamps at 20° ± 2° C.), over 70 per cent of the colonies of *P. pseudovolvox* produced eight-celled daughter colonies and in a considerable number grand-daughter colonies developed before dissolution of the parental membrane. In *P. elegans* no eight-celled daughter colonies nor grand-daughter colonies arose. Further, while the pseudocilia on *P. pseudovolvox* were

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[1] It has now been found that transformation of vegetative into motile cells may be induced by keeping colonies in the dark for about a week. Assumption of motility follows disintegration of the colonies into solitary cells.

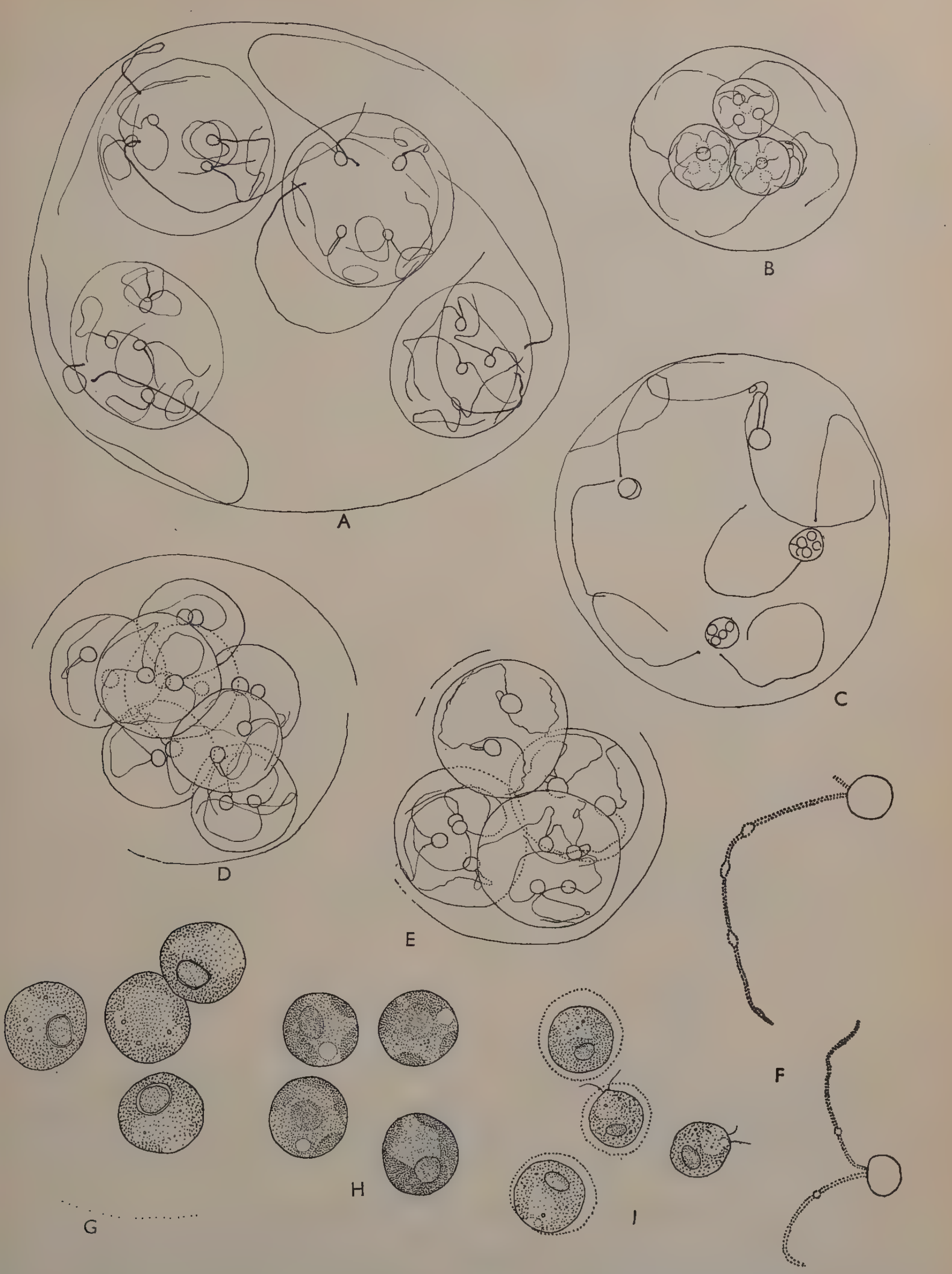

Fig. 8. *Paulschulzia elegans* (Woron.) comb.nov. A, colony with four daughter colonies each with four cells from Bassenthwaite Lake; B, similar colony from Windermere; C, D, colonies from Bassenthwaite Lake in early (C) and late (D) stages of reproduction; E, colony from Windermere, late stage in reproduction; F, pseudocilia showing inflations; G–I, typical cells from Windermere, I in culture, in H three cells seen from above; pseudocilia only shown in I. A–E, from formalin material; F, mounted in indian ink; G–I, from living material. A–E, ×270; F, ×770; G–I, ×1100.

always well developed and extended at least beyond the envelope of the daughter colony, those of *P. elegans* were either absent or very short. Lastly, *P. pseudovolvox*, but not *P. elegans*, often produces swarmers in culture, particularly if the environmental conditions are rapidly and drastically altered. Thus, though some morphological changes may arise under cultural conditions, the two algae remain clearly distinct. A culture of *P. elegans* has been deposited at the National Type Culture Collection of Algae and Protozoa at Cambridge, and material from Windermere, preserved in formalin, at the British Museum (Natural History), London, and the Windermere laboratory of the Freshwater Biological Association.

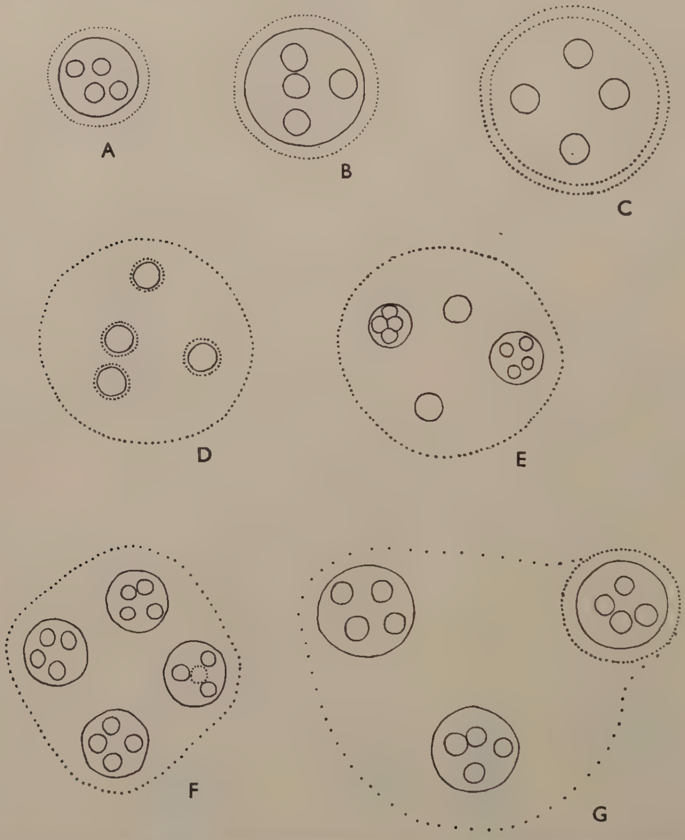

Fig. 9. *Paulschulzia elegans* (Woron.) Colony development. Only cell outlines shown. Windermere 'strain' in culture. All from living material mounted in indian ink and × 270.

The genera **Tetraspora** Link and **Paulschulzia** (Teil.) Skuja

Teiling (1942) and Skuja (1948) emphasize that *Paulschulzia* differs from *Tetraspora* in the compound nature of the colonies, the latter pointing out that, in *Tetraspora*, at the most four cells lie in a common envelope. Neither author is wholly correct. The units out of which the colonies of both genera are produced are the same. It is true that, so far as is known, the cells of *Tetraspora* do not form more than four daughter cells, the envelopes surrounding them are generally more diffluent, thus being difficult to see, and are more or less completely lost before these cells reproduce. In *Paulschulzia* these envelopes persist and are usually a prominent feature and, as has been described (p. 604), the various envelopes represent various generations.

If, eventually, species are found with the envelopes of more than four generations of cells still detectable, then the only distinction between the genera will be the presence of these envelopes. Indeed, even now, there would appear to be a case for reducing *Paulschulzia* to subgeneric rank. Ettl (1955) lays stress on the length of the pseudocilia and whether they extend beyond the colonial envelope; in *Tetraspora* they are short (two to four times as long as the cell) and do not extend beyond the mucilage. On this view, *Paulschulzia elegans* might be placed in either genus. Since, also, there is disagreement as to whether the second character he uses is universal (see Ettl, 1955, p. 48), and in any case the length of the pseudocilium is scarcely worthy of being a generic character and, in my view, varies more than he suggests, I doubt whether we are justified in removing species from *Tetraspora* because they lack these two characters. Hence, until more is known of its development, it must remain uncertain whether *Tetraspora lamellosa* Prescott (see Prescott, 1951) belongs to this genus, *Paulschulzia* or *Fottiella* Ettl (1955). The last genus seems to me to differ from the other two most clearly in two features which are not known to be present in *Tetraspora lamellosa*, namely that all the pseudocilia point in the same direction and that reproduction is solely by motile cells, two features which make this genus easy to distinguish from *Tetraspora* or *Paulschulzia*.

Dr Hannah Croasdale has kindly translated the diagnoses of new taxa into Latin.

Diagnoses

Radiococcus planktonicus sp.nov.

Colonies (to 250 μ length) of rounded but more or less irregular shape. Cells (4–7 μ diam.) globose, distributed at random in the structureless mucilage, commonly in tetrads, also in pairs or singly. Chromatophore parietal, basin-shaped, pyrenoid basal. No contractile vacuoles or stigma. Reproduction by four or two autospores per cell.

In the plankton of Windermere (type locality) and other lakes in the English Lake District.

Coloniae (ad 250 μ long.) forma subirregulariter rotundatae. Cellulae (4–7 μ diam.) globosae, in mucilagine sine structura fortuite distributae, plerumque quaternae, etiam binae vel singulae. Chromatophorus parietalis trulliformis, pyrenoideo basali. Vacuolae pulsantes stigmaque desunt. Reproductio per quattuor vel duas autosporas in cellula.

In plankto lacus dicti Windermere (loco typi) atque aliorum lacuum in regione Lacuum Anglicorum.

Elakatothrix gelatinosa Wille var. **aplanospora** var.nov.

Smaller colonies, elliptical, fusiform or cylindrical; larger ones (to 260 μ length, 170 μ breadth) of more or less irregular shape. Cells (12–36 μ length, 3–4 μ breadth) with one, rarely two, parietal chromatophores and one or two pyrenoids. Aplanospores (to 11 μ diam.) produced singly from each cell, globose, at first with two contractile vacuoles, liberated by dissolution of the mother cell wall over the central region of the cell.

Coloniae minores ellipticae, fusiformes aut cylindricae; maiores (ad 260 μ long., 170 μ lat.) forma subirregulares. Cellulae (12–36 μ long., 3–4 μ lat.) chromatophoris parietalibus uno, raro duobus, et pyrenoideis uno vel duobus praeditae. Aplanosporae (ad 11 μ diam.) singulae a cellula factae, globosae, primum duabus vacuolis pulsantibus praeditae, per dissolutionem tegumenti cellulae parentis super regionem centralem cellulae liberatae.

Paulschulzia elegans (Woron.) comb.nov. (*Tetraspora elegans* Woron.) (enlarged diagnosis)

Colonies (to 200 μ diam.) globose to oval, containing two to eight cells or daughter colonies. Mucilage envelope with or without two layers, the outer usually less than

10 μ diam. Cells (to 15 μ diam.) globose, more or less widely spaced from one another. Pseudocilia (to 190 μ length) two per cell, lying within the envelope of the colony (or daughter colony). Chromatophore parietal, basin-shaped or somewhat irregular in shape with a basal pyrenoid. Two contractile vacuoles; no stigma. Autospores two to eight per cell. Zoospores unknown (see footnote p. 608).

River Boljšaja Nevka, near Leningrad, Russia (type locality) and lakes in the English Lake District.

Coloniae (ad 200 μ diam.) globosae ad ovatae, 2–8 cellulas aut colonias-filias continentes. Involucrum mucosum cum vel sine stratis duobus, strato exteriore plerumque minore quam 10 μ diam. Cellulae (ad 15 μ diam.) globosae, aliquantulum late dispositae. Pseudocilia (ad 190 μ long.) duo in cellula, intra involucrum coloniae (vel coloniae-filiae) sita. Chromatophorus parietalis, trulliformis aut forma subirregularis, pyrenoideum basale habens. Cellula cum duabus vacuolis pulsantibus, sine stigmate. Autosporae 2–8 in cellula. Zoosporae non repertae (see footnote p. 608).

In fluminae dicto Boljšaja Nevka ad Leningrad, in Russia (loco typi) necnon in lacubus in regione Lacuum Anglicorum.

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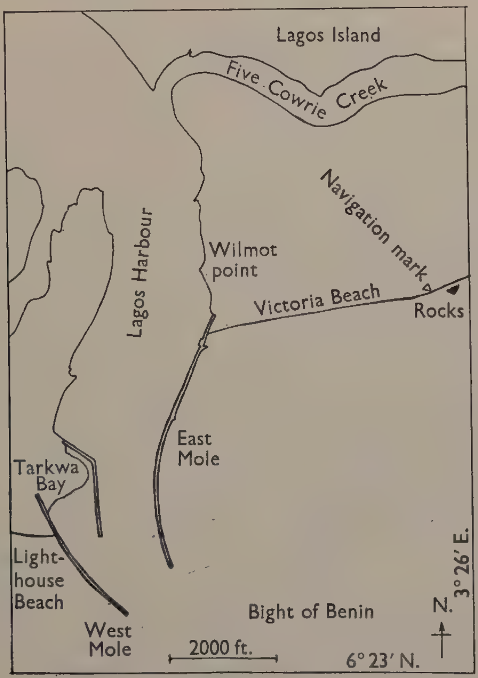
A first list of marine algae from Nigeria. By MARGARET FOX

(With Plate 54 and 5 Text-figures)

[Read 24 May 1957]

In a search of the literature on marine algae from West Africa I have been able to trace only one previously published work on marine algae from Nigeria. This is Mills (1932): 'Some diatoms from Warri, South Nigeria', and deals with both marine and fresh-water forms. The marine algae of the Cameroons were listed by Pilger (1911). Recently, Lawson (1955) made an ecological survey of the rocky shores of the Cameroons, and reports several species not found by Pilger. Even so, there are only nine species in common between Lagos and the Cameroons. There are three papers listing the marine algal flora of San Thomé (Henriques, 1885, 1886; Hariot, 1908), but there are only four species in common between San Thomé and Lagos.

The algae listed here were collected between 1953 and 1956, principally at Lagos, Nigeria, although one collection made in October 1954 at Freetown, Sierra Leone, and another made in January 1954 at Port Harcourt, Nigeria, are included.



Text-fig. 1

At Lagos algae grow on the pegmatite boulders forming the East and West Moles protecting the harbour (see map, Text-fig. 1). Collections were made in the following places in the months indicated:

West Mole, Lighthouse Beach side, in March and November 1953, March and November 1954 and January 1956.

West Mole, Tarkwa Bay side, in March, April and November 1953, March and November 1954 and January 1956.

East Mole, Victoria Beach side, in March, April and November 1953, March and November 1954 and January 1956.

Victoria Beach rocks (an artificial reef about one mile east of the East Mole, along Victoria Beach) in March and April 1954. By November 1954 the reef was not visible.

Algae have not been observed so far on the other more protected parts of the harbour works.

The plankton collections of Mr C. I. O. Olaniyan, B.Sc., of the Department of Zoology, University College, Ibadan, were very kindly made available for the identification of phytoplankton. These samples consisted of collections made at both high and low tide in each of three places at Lagos (in the harbour entrance, off Wilmot Point, in Lagos Lagoon off Onikan Beach) in January, March, June and September 1954. The samples are not comparable quantitatively.

One collection was made at Ikoyi Beach, Lagos Lagoon (no. 45) and one was made in the brackish swamp dominated by *Avicennia germinans* (L.) Stearn, behind Tarkwa Bay (no. 56). The remaining Nigerian collection is from the brackish water creeks round Port Harcourt (nos. 3 and 19).

In Sierra Leone one collection was made at Man o' War Bay, near Freetown (nos. 49, 50, 52 and 53).

In describing ecological conditions at Lagos the following summary of tidal data is relevant:

Max. (theoretical) tidal range (high water springs to low water springs), 4·8 ft.

Max. (actual) tidal range (high water springs to the following low water) (December), 4·5 ft.

Min. tidal range between two succeeding tides (March), 0·9 ft.

Average tidal range throughout the year, 2·5 ft.

Climate and weather play a larger part in determining the distribution of algae than is the case in a temperate region. The drying sea breeze and intense insolation along the shore preclude algal growth anywhere which is above surf or wave wash for two hours or more at low water. Wave height is always more than the average tidal range, generally several times more, and this makes for heavy surf action. Theoretically the lowest tides run in May to July at night, and it is also impossible to collect during the daytime in this period because of the high seas associated with the onset of the rains.

Broadly speaking there are two ecological groups of plants on the Moles at Lagos; there is the group which will withstand the complete absence of sea water, including surf and wave wash, for about two hours at low water, and there is another much larger group of species which cannot withstand this kind of exposure at all. The first group, of *Chaetomorpha antennina*, *Enteromorpha clathrata* and *Bachelotia fulvescens*, is found on rocks at the base of the landward end of the Moles, where the sand is often shifting, and forms a 'landward limit of algal growth'. This same group of species is also to be found at the vertical upper limit of algal growth in the surf zone, the habitat of the second group of species, consisting of *Bryopsis stenoptera*, *Ectocarpus* spp., *Chnoospora minima*, *Gracilaria dentata*, *Hypnea musciformis* and *Bryocladia thyrsigera*. The surf zone here may be defined as 'that region (of a Mole) which has as its vertical lower limit low-water level and as its vertical upper limit a level which is kept constantly moist by surf or wave wash'; the zone extends horizontally seaward from a point at which most of the waves have broken at low water.

The emersion which the first group of species is able to withstand may not be as severe as it would seem, since the three species concerned generally grow through and over sand, and moisture is probably available from below. Of the second group of species, the first three species tend to be found towards the vertical upper limit of the surf zone, and the last three species towards its lower limit, but the clear zonations found in temperate regions cannot be distinguished.

Sourie (1954), in a study of the marine ecology of four places in Senegal (including Mauritania and French Guinea), distinguishes a horizontal distribution of algae, determined by the degree of moisture maintained by the interaction of tide and waves, and a vertical zonation determined by the degree of exposure ('très battu', 'battu' and 'abrité'). These regions can only be observed in the most general terms at Lagos where the flora is essentially a limited one.

Among the diatoms of the phytoplankton the occurrence of a fresh-water form, *Melosira granulata* (Ehrenb.) Ralfs, reflecting the large amounts of fresh water entering the harbour as a result of the rains, is interesting. The months of the phytoplankton samples were chosen arbitrarily, and salinity records made available subsequently by the Department of Zoology, University College, Ibadan, suggest that a better choice is possible. But in the collections listed here, *M. granulata* has been found in the samples taken at low water in June 1954 in the harbour entrance, off Wilmot Point and in Lagos Lagoon; and also at both high and low water in September 1954 in samples from Wilmot Point and Lagos Lagoon. Salinities in the harbour entrance range from about 25 to 35 % all the year round at high tide and also at low tide in the dry season. At low tide in the rains and just after the value drops to about 5 %. The other diatoms are marine and brackish-water forms, mostly cosmopolitan in distribution, except *Radiodiscus hispidus* (Grun.) Mills, which has a rather sporadic distribution (Voigt, 1951), and has been previously reported from Nigeria (Mills, 1932).

I am most grateful to Dr C. Bliding, who has identified specimens belonging to the genus *Enteromorpha*, to Dr Th. J. Koster (Cladophora), to Mr R. Ross (Diatoms), and to Mr F. Drouet (Myxophyceae). The collections were made while I was attached to the Department of Botany, University College, Ibadan, and I wish to thank Prof. F. W. Sansome for the facilities provided. Special thanks are due to the Keeper of Botany at the British Museum (Natural History), where I worked for several most agreeable months, and to his staff.

In commenting on each species I have tried to give some idea of what is thought to be its distribution on the Atlantic coast of Africa and in the West African islands. I have included the east coast of South Africa, which is swept by a warm current, and this distribution is referred to in the text simply as 'Africa' for brevity. There have been very few authentic herbarium specimens available to me in this connexion, except those of Welwitsch from Angola, and the records are in many cases taken from papers dating from over forty years ago; these are all included in the list of works referred to at the end of the paper. I have included a minimum of synonymy to cover the names used in these papers where they differ from the ones in current use. Recent lists, mentioning species I have found so far at Lagos, have appeared for Morocco (Dangeard, 1949), Senegal (Sourie, 1954), Sierra Leone (Lawson, 1954), the Gold Coast (Dickinson & Foote, 1950–1; Dickinson, 1951–2), Cameroons (Lawson, 1955) and South Africa (Kylin, 1938; Levring, 1938; Papenfuss, 1943 etc.; Stephenson, 1948).

Thirty-six species are listed here, excluding diatoms; chiefly for reason of inadequate material I have omitted for the time being twelve other species. Fourteen species of diatoms are listed, and there are about ten more species which occur sporadically in plankton and as epiphytes.

CHLOROPHYCEAE

ULVACEAE

Enteromorpha Link, 1820

Enteromorpha clathrata (Roth) Grev., *Alg. Brit.* p. 181 (1850), in sensu Bliding, *Bot. Notiser*, p. 331 (1944)

This is a very variable species as found at Lagos. In exposed conditions at the landward limit of algal growth it appears as fine pale green threads often growing through sand, and with smaller cells than is typical. This material Dr Bliding has identified as

E. clathrata (group) (nos. 2.88 and 2.90). In the surf zone (no. 2.89) the plants may look the same macroscopically as those growing higher up, or the growth may be of a much coarser, brighter green kind (no. 4 from the more sheltered conditions of Tarkwa Bay), but the cell size, Dr Bliding considers, is more typical. No. 5 (West Mole, Lighthouse Beach, March 1954) shows a cell size most nearly like that of most European material. Text-figs. 2 and 3 illustrate the difference in cell size between nos. 2.90 and 5. *E. clathrata* generally has 4–7 pyrenoids in each cell.

At Man o' War Bay *E. clathrata* (group), again with small cells, was found on the scoriaceous rock exposed at low tide (no. 49) and on pebbles in the fresh-water streams that flow into the bay at low water (no. 53, with larger cells).

Materials. Nos. 2 (spirit), 2.88, 2.89, 2.90, 4, 146, 157, 177, (Lagos); 49, 53 (spirit, Freetown).

Distribution. Africa—South Africa, Ascension, Annobon, Nigeria, Sierra Leone, Cap Vert Is., Canary Is., Morocco, Tangier. Elsewhere very widely spread in most waters, but it is improbable that all the material giving rise to those records is *E. clathrata* in sensu Bliding.

Enteromorpha intermedia Bliding, *Bot. Notiser*, **108** (2), 253 (1955)

This new species was founded by Dr Bliding on material from Europe. In Nigeria it has been found growing with *E. clathrata* tangled round the roots of *Rhizophora* spp. in the creeks round Port Harcourt. The cells are rather square and have 1–2 pyrenoids each (Text-fig. 4). No. 193 is also from a brackish-water habitat, though no. 190 was found in the surf zone on the shore. *E. intermedia* has not been previously reported from the Gold Coast.

Material. No. 3 (spirit, Port Harcourt); 190 (Gold Coast, Tema); 193 (Lagos).

Distribution. Africa—Nigeria, Gold Coast. Sweden, Holland, England and Wales, U.S.A.

CLADOPHORACEAE

Chaetomorpha Kütz., 1845

Chaetomorpha antennina (Bory) Kütz., *Spec. alg.* p. 379 (1849)
Chaetomorpha media (J. Ag.) Kütz., *Spec. alg.* p. 380 (1849)

Børgesen, Some marine algae from Mauritius, I, Chlorophyceae, in *K. danske vidensk. Selsk., Biol.*, **15**, (4), 37 (1940)

At Lagos the growth of this species is relatively stunted; it forms bright green shining tufts up to 7 cm. high, both at the landward limit of algal growth and towards the vertical upper limit of the surf zone. The basal cell is up to 2·5 mm. long, about 150μ wide at its base and 240μ wide at the top. In the filaments the cells are 390–500μ wide by 1–3 times longer.

At Man o' War Bay *C. antennina* is common in the pools in the basalt rock surrounding the Bay, near high-tide level, and on the pebbles in the fresh-water streams running into the Bay at low water.

Material. Nos. 6, 152 (Lagos); 53 (spirit, Freetown).

Distribution. Africa—South Africa, Cameroons, Nigeria, Gold Coast, Sierra Leone, Senegal, Cap Vert Is., Canary Is. Widespread in warmer seas elsewhere.

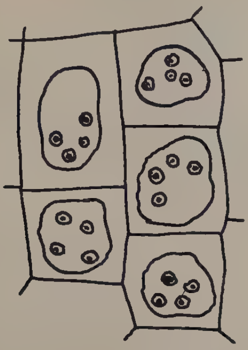
Cladophora Kütz., 1843

Cladophora albida (Huds.) Kütz., *Phyc. gen.* p. 267 (1843)
Cladophora tenuis Kütz., *Phyc. germ.* p. 209 (1845)

This species has been found only on rocks in the surf zone in the more protected conditions of Tarkwa Bay. Reported previously in Africa only from the Cameroons by Pilger (1911).

Material. Nos. 92, 159 (Lagos); 137 (Gold Coast, Pram Pram).

Distribution. Africa—Cameroons, Nigeria, Gold Coast. Atlantic and Mediterranean coasts of Europe, Atlantic coast of North America south to Brazil, West Indies, Indian Ocean, Viêt Nam, Australia.



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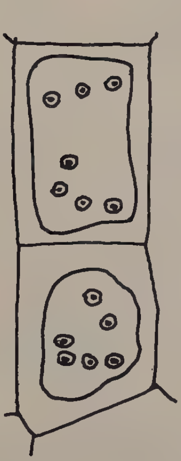

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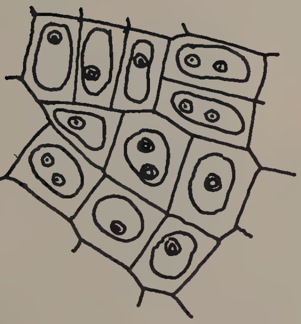

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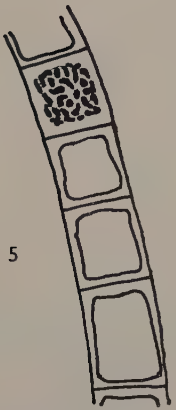

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Text-fig. 2. *Enteromorpha clathrata* (group), no. 2.90. (×832.)
Text-fig. 3. *Enteromorpha clathrata*, no. 5. (×832.)
Text-fig. 4. *Enteromorpha intermedia*, no. 3. (×832.)
Text-fig. 5. *Lola tortuosa* (×296.)

Cladophora fascicularis (Mert.) Kütz., *Phyc. gen.* p. 268 (1843)

On the whole *C. fascicularis* grows in more exposed situations than *C. albida*. It is common on rocks at the landward end of the surf zone on the outer faces of the Moles, and on Victoria Beach rocks.

Material. Nos. 69, 93 and 41, 42 (spirit) (Lagos), 136 (Gold Coast, Pram Pram).

Distribution. Africa—Nigeria, Gold Coast, Cap Vert Is., Canary Is., Morocco. Apparently pantropical and subtropical.

Lola Hamel, 1939

Lola tortuosa (Dillw.) Chapman, *J. Linn. Soc., Bot.*, **55**, 463 (1956)
Rhizoclonium tortuosa (Dillw.) Kütz., *Phyc. germ.* p. 205 (1845)

The cells of the filaments are mostly 34–40μ wide by 1½ times as long (Text-fig. 5).

MATERIAL. No. 1 (Lagos).

DISTRIBUTION. Africa—South Africa, Nigeria. Widely spread in most seas.

Rhizoclonium Kütz. 1843

Rhizoclonium implexum (Dillw.) Kütz., Koster, The genus Rhizoclonium Kütz. in the Netherlands, in *Pubbl. Staz. Zool. Napoli*, **27**, 343 (1955)
Rhizoclonium kochianum Kütz., *Phyc. germ.* p. 206 (1845); Stockmeyer, Ueber die Algengattung Rhizoclonium, in *Verhandl. zool.-bot. Ges. Wien*, **40**, 582 (1890)
Rhizoclonium kerneri Stockm.

At Lagos this species occurs tangled with other species in the surf zone; at Port Harcourt it was found twisted round the roots of *Rhizophora* spp. in the brackish water of the creeks. It was also found at Man o' War Bay in the streams flowing into the Bay at low water.

The cells are fairly evenly 15μ wide by 1¼–3 times as long, usually 2–2½ times; in the Port Harcourt material cell width varied from 15 to 22μ.

MATERIAL. No. 7 (Lagos); 3, 19 (spirit, Port Harcourt); 53 (spirit, Freetown).

DISTRIBUTION. Africa—Nigeria, Sierra Leone, Morocco. Known from the West Indies and Europe, Persian Gulf and Indian Ocean.

BRYOPSIDACEAE

Bryopsis Lam. 1809

Bryopsis pennata Lam., *Nouv. Bull. Sci. Soc. Philom.* **1**, 333 (1807)

It seems that there are two species of *Bryopsis* growing intermingled at Lagos. Together they form a dull green fringe on turf on rocks in the surf zone, particularly in Tarkwa Bay, which is very sheltered. There are no intermediates between the two kinds, and the larger seems to be fairly typical *B. pennata*. Lawson nos. A903 and A968 from Freetown are also *B. pennata*.

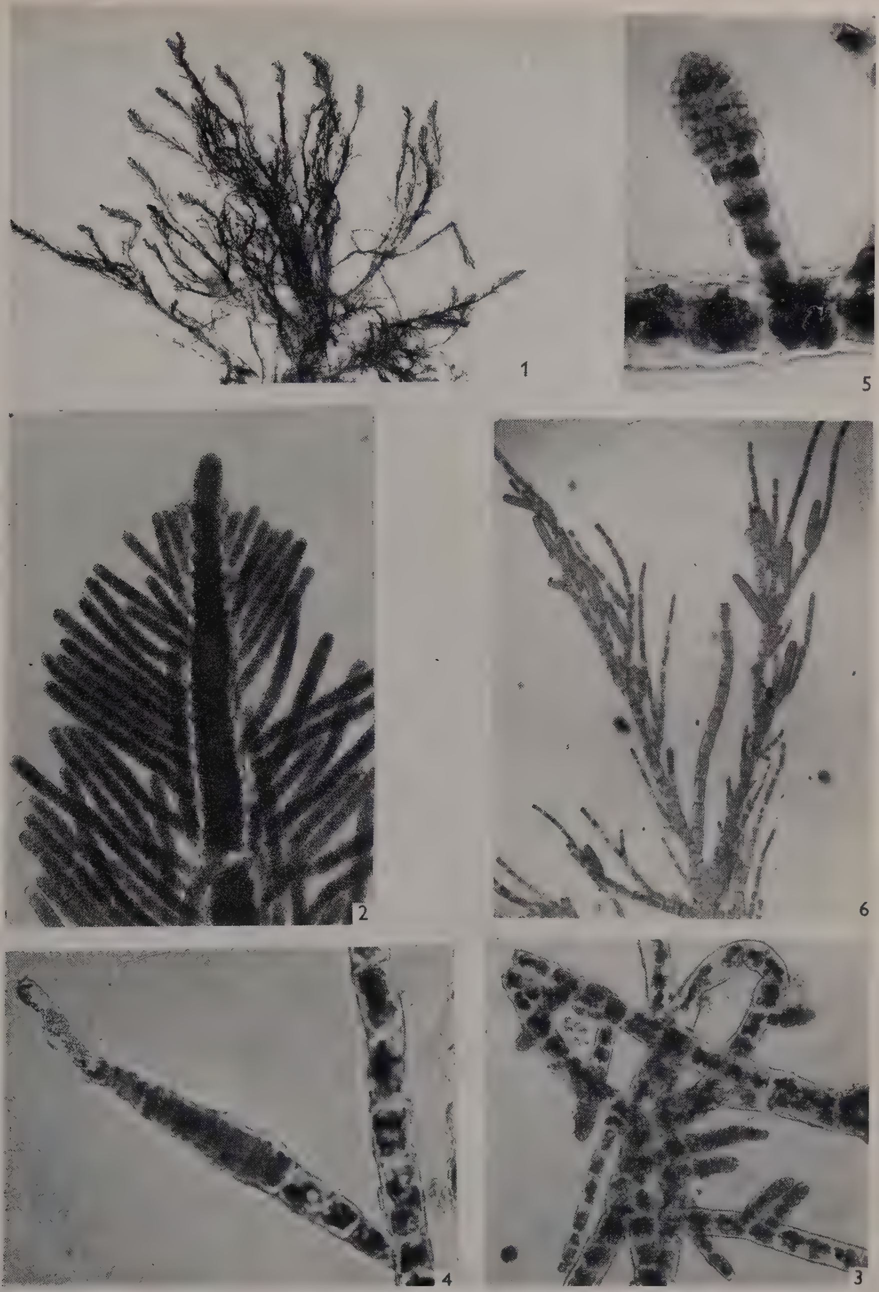
MATERIAL. Nos. 8, 170 (Lagos).

DISTRIBUTION. Africa—Angola, Nigeria, Gold Coast, Sierra Leone, Senegal, Morocco. Warmer Atlantic shores of America, West Indies and Ceylon.

Bryopsis stenoptera Pilger, Die Meeresalgen von Kamerun, in *Bot. Jb.* **46**, 295 (1911–12)

This species is altogether much finer than *B. pennata*. It forms part of the same turf, up to 3 cm. high, but its measurements are much less. A specimen of the material on which Pilger's description was based (Ledermann no. 557) was found in Herb. Børgesen in Copenhagen, and recent Cameroons, Nigerian and Gold Coast material compared with it. The Cameroons material (Lawson nos. A751, A807 and A847) all proved to be *B. stenoptera*, and so did the Nigerian material. None of the Gold Coast material belonged to this species (Lawson nos. A248, A319, A332, A353, A413, A538, A903, A921, A968, A1009, A1065, A1073).

The plants are characterized by the linear-lanceolate fronds with fine, crowded distichously arranged pinnae (Pl. **54**, fig. 1). The main axes are little branched, loosely interwoven, mostly 150–260μ wide at the base and about 80μ wide in the frond. The pinnae are fairly regularly 36μ wide; they are evenly cylindrical (except at base and



Figs. 1–2. *Bryopsis.*
Figs. 3–5. *Bachelotia.*
Fig. 6. *Ectocarpus.*

(*Facing p.* 620)

apex) throughout their length, of more or less the same length, and very closely set on the axis of the frond (see Pl. **54**, fig. 2). The pinnae are present for a considerable distance down the axis, usually, giving it a shaggy appearance, and after they have fallen away their scars are visible almost to the rhizoidal base.

MATERIAL. Nos. 8, 170 (Lagos).

DISTRIBUTION. Africa—Cameroons, Nigeria.

PHAEOPHYCEAE

ECTOCARPACEAE

Bachelotia (Bornet) Fox, gen.nov.

Pylaiella subgen. *Bachelotia* Bornet, *Rev. gen. Bot.* **1**, 5 (1889)

Type species: *B. fulvescens* (Schousb. ex Bornet) Fox infra. 'A pylaiella differt sporangiis plurilocularibus terminalibus vel pilo superati, chromatophoriis stellatis.'

Bornet (loc. cit.) made his subgenus *Bachelotia* on the grounds of the different growth habit of *Pylaiella fulvescens* (and two other species) from that found in other species of the genus *Pylaiella*. Kuckuck (1930) seems to have had the same opinion, for in his posthumous *Fragmente einer Monographie der Phaeosporeen* he uses, in an incidental mention, the name *Bachelotia fulvescens*. Hamel (1939), 'Sur la classification des Ectocarpales' in *Bot. Notiser*, 1939, (1), 66) uses the name *Bachelotia fulvescens* (Schousb.) Kuckuck, as if Kuckuck had in fact published the name in a valid sense.

Bachelotia fulvescens (Schousb. ex Bornet) Fox, comb.nov.
Pylaiella fulvescens Schousb. ex Bornet, in *Rev. gen. Bot.* **1**, 5 (1889)

At Lagos this alga grows in soft brown fringes on rocks in the surf zone, or through sand over rocks at the landward limit of algal growth on the shore. At Man o' War Bay it was found in the sterile condition growing on pebbles in the fresh-water streams running into the Bay at low water.

Collections in March and April at Lagos showed intercalary unilocular sporangia, while those taken in November show a great many plurilocular sporangia. These have been recorded before, by Schiffner (1938) in material from the Laguna de Venezia (Schiffner no. 1198 in Herb. Brit. Mus.). Schiffner describes them as 'ectocarpoid' but gives no precise details.

In the Lagos material the plurilocular sporangia are solitary and sessile or terminal on a short stalk (Pl. **54**, figs. 3–5). Intercalary plurilocular sporangia are rare. Tapering cylindrical sporangia with (Pl. **54**, fig. 4) or without (Pl. **54**, fig. 3, in the centre of the photograph) a terminal hair are frequent. This kind of sporangium generally measures 80–115 μ long by 25–35 μ wide. Cylindrical sporangia each with a rounded apex are most common (see the two sporangia in the lower righthand corner of the photograph, Pl. **54**, fig. 3). These measure 50–60 μ long by 22–28 μ wide. There are also some pointed or even globose sporangia, always stalked, in which length and breadth can be equal although these usually measure 27–37 μ long by 22–27 μ wide (Pl. **54**, fig. 5).

MATERIAL. Nos. 12, 12.94, 12.98, 156, 165, 172 (Lagos), 53 (spirit, Freetown).

DISTRIBUTION. Africa—South Africa, Nigeria, Gold Coast, Sierra Leone, Senegal, Canary Is., Morocco, Tangier. Warmer coasts of Europe, West Indies, Brazil, Australia, China.

Ectocarpus Lyngbye 1819

Ectocarpus breviarticulatus J. Ag., Nya alger från Mexico, in *Öfvers. Vetensk.Akad. Förh., Stockh.*, 1847, 7 (1848). Børgesen, Marine algae of the Danish West Indies, II, Phaeophyceae, in *Dansk. Bot. Ark.* **2** (2), 173 (1914). Børgesen, Some marine algae from Mauritius, II, in *K. danske vidensk. Selsk., Biol.*, **16** (3), 39 (1941)

This is a species of characteristic appearance, forming thick tangled tresses up to 5 cm. long on rocks in the surf zone. It was found with megasporangia in all collections.

MATERIAL. Nos. 13, 13.111, 150, 153, 171, 179 (Lagos).

DISTRIBUTION. Africa—Nigeria, Gold Coast, Cap Vert Is. Widely spread in warmer seas.

Ectocarpus indicus Sonder, in Zollinger, *Syst. Verz. Zollinger, Indisch. Archipel. Japan ges. Pflanz.* (1854–5). Børgesen, Some marine algae from Mauritius, II, Phaeophyceae, in *K. danske vidensk. Selsk., Biol.*, **16** (3), 16 (1941)

Ectocarpus duchassaingianus Grunow, Reise Osterreich. *Freg. Novara, Bot.* 45 (1870). Børgesen, Marine algae of the Danish West Indies, in *Dansk Bot. Ark.* **2** (2), 159 (1914)

This material was found growing on shells attached to rocks in the surf zone in Tarkwa Bay in March 1954. Most of it is sterile, very sparsely branched, and, in contrast to *Giffordia mitchellae*, only faintly pigmented. The main axes are up to 32 μ wide, and the lateral branches taper from about 12 μ wide near their base to 5 μ at the apex. The branches of the young plants show very slight constriction at their septa.

The older plants bearing plurilocular sporangia are much more branched (Pl. **54**, fig. 6). The main axes vary from 35 to 42 μ wide and the cells are all decidedly barrel-shaped. The sporangia are mostly 15–20 and 80–160 μ long and the outline of each sporangium is uneven. Thus the sporangia present quite a different appearance from those of *Giffordia mitchellae*. The loculi are 5–7·5 μ high.

MATERIAL. Nos. 11 (spirit), 11.95, 11.96 (Lagos).

DISTRIBUTION. Africa—Nigeria. Widely spread in the warmer parts of the Atlantic, Indian and Pacific Oceans.

Giffordia (Batters) Hamel 1939

Giffordia mitchellae (Harv.) Hamel, *Phaeophycées de France*, p. 29 (1931–9)

Ectocarpus mitchellae Harv., *Ner. Bor. Amer.* **1**, 142 (1858). Børgesen, Some marine algae from Mauritius, II, Phaeophyceae, in *K. danske vidensk. Selsk., Biol.*, **16** (3), 7 (1941)

Ectocarpus virescens Thuret ex Sauvageau, Sur l'*Ectocarpus virescens*, in *J. Bot., Paris*, **10** (6), 98 and (7), 113 (1896). Børgesen, Marine algae from the Canary Islands, II, Phaeophyceae, in *K. danske vidensk. Selsk., Biol.*, **6** (2), 18 (1926)

This species was gathered at Lagos in March 1954 from both the Tarkwa Bay and Lighthouse Beach sides of the West Mole. It formed a soft greenish growth on rocks in the surf zone. Both nos. 9 and 10 were collected on both sides of the Mole, and it seems probable that no. 9 is merely a young form of no. 10.

The main axes are about 30 μ wide, the cells being 1–3 times longer than wide. Lateral branches are about 20 μ wide down to about 5 μ where they taper terminally into hairs, when the cells are 4–5 times as long as wide. There is only very slight constriction at the septa.

The meiosporangia are generally borne near the origin of a lateral branch on its anterior face. They are always cylindrical with a rounded apex, the larger ones tending to be a little broader towards the base. Mature sporangia are usually 18–20 μ wide and 50–80 μ long. The loculi are 5–7·5 μ high. No. 155 has megasporangia. (January, 1956.)

Pilger's specimen of *Ectocarpus indicus* Sond. from the Cameroons (Pilger, 1911) may in fact be *Giffordia mitchellae*. He says of it that it has 'dense fascicles of richly ramified branches', which is more typical of *G. mitchellae* than *Ectocarpus indicus*.

MATERIAL. Nos. 9, 10, 10.115, 155 (Lagos).

DISTRIBUTION. Africa—Cameroons, Nigeria, Senegal, Canary Is., Morocco, Azores. Europe, North America, West Indies, Hawaii and Marshall Is., Viêt Nam.

ENCOELIACEAE

Chnoospora J. Ag., 1847

Chnoospora minima Hering, Papenfuss, Notes on South African Marine algae, IV, in *J. S. Afr. Bot.* **22**, 69 (1956)
Chnoospora pacifica J. Ag., Nya alger från Mexico, in *Öfvers. Vetensk.Akad. Förh., Stockh.*, 1847, **7** (1848)
Chnoospora fastigiata var. *pacifica* J. Ag., *Spec. Alg.* **1**, 172 (1848)

This is a very common alga at Lagos, growing attached to rocks in the upper part of the surf zone. The fronds are mostly 5–20 cm. long, and the apices are rounded, never attenuate. In habit the specimens agree very well with the plant illustrated by Levring (1938, pl. IV, fig. 12) from the east coast of South Africa. The fronds in my material are somewhat compressed throughout their length; they do not form cushions nor is there any sign of dilation below the axils.

MATERIALS. Nos. 24, 24.101, 24.102, 151, 154, 178 (Lagos).

DISTRIBUTION. Africa—South Africa, Annobon, Nigeria, Cap Vert Is. Warmer waters of the Pacific and Indian Oceans, Australia.

STYPOCAULACEAE

Halopteris (Kütz.) Sauv., 1903

Halopteris scoparia (L.) Sauv., Remarques sur les Sphacélariacées, in *J. Bot., Paris*, **17** (12), 378 (1903)
Stypocaulon scoparium (L.) Kütz., *Phyc. gen.* p. 293 (1843)

This alga was found only once in the sterile condition on Victoria Beach rocks, where it was constantly wave washed.

MATERIAL. No. 14 (Lagos).

DISTRIBUTION. Africa—South Africa (Barton), Nigeria, Canary Is., Madeira, Grand Desert and Salvage Is., Morocco, Tangier, Azores. Shores of Europe, North Africa, North America, West Indies, Australia.

DICTYOTACEAE

Dictyopteris Lam., 1809

Dictyopteris delicatula Lam., in *Nouv. Bull. Sci. Soc. Philom.* **1**, 332, pl. 6, fig. 2*b* (1809)
Haliseris delicatula (Lam.) J. Ag., *Spec. alg.* **1**, 116 (1848)

Occasionally found as solitary tufts in the surf zone.

MATERIAL. No. 99 (Lagos).

DISTRIBUTION. Africa—South Africa, Nigeria, Gold Coast, Senegal, Cap Vert Is. Atlantic coast of America from the Gulf of Mexico to Brazil, W. Indies.

Dictyota Lam., 1809

Dictyota ciliata J. Ag., *Linnea*, **15**, 5 (1841). Dickinson, Marine algae from the Gold Coast, IV, in *Kew Bull.* p. 41 (1952).

So far this species has only been found washed up at Lagos.

MATERIAL. No. 100 (Lagos).

DISTRIBUTION. Africa—S. Thomé, Rolas, Nigeria, Gold Coast. Tropical Atlantic and Indian Oceans, Red Sea, Malay Archipelago and Australia.

RHODOPHYCEAE

GONIOTRICHACEAE

Goniotrichum Kütz., 1843

Goniotrichum elegans (Chauv.) Le Jolis, *Liste des algues marines de Cherbourg*, p. 103 (1863)
Goniotrichum alsidii (Zanard.) Howe, Marine algae of Peru, in *Mem. Torrey bot. Cl.* **15**, 75 (1914)

A fairly common epiphyte appearing in several collections. The filaments are 15–18 μ wide throughout the greater part of their length.

MATERIAL. Nos. 7 and 41, 42 (spirit) (Lagos).

DISTRIBUTION. Africa—South Africa, Nigeria, Senegal, Canary Is., Morocco, Azores. Cosmopolitan.

ERYTHROPELTIDACEAE

Erythrocladia Rosenv., 1909

Erythrocladia subintegra Rosenvinge, Marine algae of Denmark, I, in *K. danske vidensk. Selsk. Skrift.* **7**, 7 (1), 73 (1909)

An epiphyte which often occurs on *Chaetomorpha antennina*, *Cladophora fascicularis*, *Bostrychia simpliciuscula*, etc. Numerous hemispherical spores 5 μ in diameter, together with several stages in germination, were found on *Polysiphonia ferulacea*.

MATERIAL. Nos. 6, 38, 56, 93 (Lagos).

DISTRIBUTION. Africa—Nigeria, Senegal, Morocco. Probably cosmopolitan.

GELIDIACEAE

Gelidium Lam., 1813

Gelidium pusillum (Stackh.) Le Jolis, Liste des algues marines de Cherbourg, in *Mém. Soc. Sci. Nat. Cherbourg*, **10**, 139 (1864)

This species forms a red turf on rocks in the surf zone on both sides of the West Mole at Lagos, particularly in Tarkwa Bay where it has increased greatly in the last three years.

MATERIAL. Nos. 17.101, 21, 48, 164, 174, 175 (Lagos).

DISTRIBUTION. Africa—Cameroons, Nigeria, Gold Coast, Sierra Leone, Senegal, Cap Vert Is., Azores. Mediterranean and Atlantic coasts of Europe, Mauritius, Japan. Widely spread in temperate and tropical seas.

HYPNACEAE

Hypnea Lam., 1913

Hypnea musciformis (Wulf.) Lam., *Essai...des Thallassiophytes*, p. 43 (1813)

This is a very common constituent of the turf on the rocks of the surf zone. It has usually been found with both antheridia and cystocarps in March.

MATERIAL. Nos. 55, 168, 169 (Lagos),

DISTRIBUTION. Africa—South Africa?, Angola, French Equatorial Africa. S. Thomé, Cameroons, Nigeria, Gold Coast, Sierra Leone, Senegal, Cap Vert Is., Canary Is., Morocco, Azores. Very widely distributed in warmer waters elsewhere.

GRACILARIACEAE

Gracilaria Grev., 1830

Gracilaria dentata J. Ag., *Spec. alg.* **2** (2), 603 (1852). Dangeard, Algues de la presqu'île de Cap Vert (Dakar) et de ses environs, in *Botaniste*, **36** (1–6), 288 (1952)

Gracilaria henrequesiana Hariot, Les algues de S. Thomé, in *J. Bot., Paris*, sér. 2, 1, 162 (1908). Dickinson and Foote, Marine algae from the Gold Coast, I, in *Kew Bull.* (2), 270 (1950)

In determining the Lagos material I have compared it with a collection made at Pram Pram in the Gold Coast in December 1955. The Lagos material agrees best with specimens taken from pools high on the shore at Pram Pram. Here at low tide the water left in the pools becomes quite warm, and the thalli are thin and laciniate in the same way as those growing in heavy surf at Lagos. Some of the Lagos specimens agree exactly with Dangeard's illustration (loc. cit. pl. XV, figs. F–H).

Intermediates exist in the Pram Pram material between *G. henrequesiana* Hariot and *G. dentata* J. Ag., and I do not think that Hariot's species can be regarded as distinct from *G. dentata.*

MATERIAL. Nos. 22, 22.104, 22.105, 22.106, 122.107, 47, 161 (Lagos).

DISTRIBUTION. Africa—French Equatorial Africa, S. Thomé, Cameroons, Nigeria, Gold Coast, Senegal, Cap Vert Is. West Indies and Florida.

PHYLLOPHORACEAE

Gymnogongrus Martius 1833

Gymnogongrus intermedius Kylin, Verzeichnis einiger Rhodophyceen Südafrikas, in *Acta Univ. Lund.* (N.F.), **49** (8), 12 (1938)

The plants form crisp brownish tufts on rocks low in the surf zone, they are up to 3 cm. high, fastigiate with terete fronds 0·5 mm. (or a little more) across. Branching is regularly dichotomous only distally. The cystocarps are immersed in the thallus.

MATERIAL. Nos. 20 (spirit), 57 (Lagos).

DISTRIBUTION. Africa—South Africa, Nigeria.

Gymnogongrus tenuis J. Ag., *Acta Holm.* p. 88 (1849)

The reddish black tufts of this species are not uncommon on particularly exposed rock faces in the surf zone. The tufts are 2–3 cm. high and very fastigiate.

MATERIAL. No. 58, 149 (Lagos).

DISTRIBUTION. Africa—Nigeria, Senegal. West Indies, Pacific coast of Mexico, California.

CORALLINACEAE

Jania Lam., 1812

Jania rubens (L.) Lam., *Hist. Polyp. corall. flex.* p. 272 (1816)
Corallina rubens L., *Fauna Suec.* ed. 2, 540 (1761).

Rare, only growing among the basal parts of *Bryocladia thyrsigera.* Some of the terminal segments of this material are unusually long, up to 20 times their width.

MATERIAL. No. 23 (Lagos).

DISTRIBUTION. Africa—South Africa, Cameroons, Nigeria, Senegal, Cap Vert Is., Canary Is., Madeira, Grand Desert Is., Morocco, Azores. Norway southwards; widely spread in warmer seas generally.

CRYPTONEMIACEAE

Grateloupia C. Ag., 1822

Grateloupia filicina (Wulf.) C. Ag., *Spec. Alg.* **1**, 223 (1822)

A rare plant growing in isolated tufts on the sheltered sides of rocks near low water.

MATERIAL. No. 54, 163 (Lagos).

Distribution. Africa—South Africa, St Helena, Cameroons, Nigeria, Gold Coast, Senegal, Canary Is., Morocco, Tangier, Azores. Elsewhere very widely spread in warmer waters.

Ceramiaceae

Centroceras Kütz., 1841

Centroceras clavulatum (C. Ag.) Mont., *Explor. scient. de l'Algérie, Algues*, **1**, 140 (1846)
Centroceras cryptacanthum Kütz., *Linnea*, **15**, 741 (1841)
Centroceras hyalacanthum Kütz., in J. Ag. *Linnea*, **15**, 742 (1841)
Ceramium clavulatum C. Ag., in Kunth, *Syn. plant.* **2**, 2 (1822)

Like the preceding species, this plant has only been found occasionally among the basal parts of *Bryocladia thyrsigera*.

Material. No. 39 (spirit) (Lagos).

Distribution. Africa—South Africa, South West Africa, Angola, St Helena, Ascension, French Equatorial Africa, S. Thomé, Rolas, Annobon, Cameroons, Nigeria, Gold Coast, Liberia, Sierra Leone, Senegal, Cap Vert Is., Morocco, Madeira, Azores. Very widely distributed in warmer waters.

Rhodomelaceae

Bostrychia Mont. 1838

Bostrychia simpliciuscula Harv. ex J. Ag., *Spec. alg.* **2** (3), 854 (1863)
Bostrychia tenuis f. *simpliciuscula* (Harv. ex J. Ag.) Post, *Rev. algol.* **9**, 22 (1936)

This species grows thickly on the pneumatophores of *Avicennia germinans* (L.) Stearn, in the brackish water at the back of Tarkwa Bay. It also grows, together with another species of *Bostrychia*, on the prop roots of *Rhizophora* spp. in the creeks round Port Harcourt. The material of this other species of *Bostrychia* is insufficient for specific identification.

Material. Nos. 56 (Lagos), 19 (spirit) (Port Harcourt).

Distribution. Africa—South Africa, Nigeria. Dutch East Indies, Australia, New Zealand, Friendly Is., Chile.

Bryocladia Schmitz, 1897

Bryocladia thyrsigera (J. Ag.) Schmitz, in Falkenb. *Rhodomelaceen*, p. 169 (1901)

This plant grows abundantly at Lagos, forming dense turfs low in the surf zone. Specimens in all stages of reproduction have been found in each collection.

Material. Nos. 28, 31, 31.113, 148, 162, 165, 166.

Distribution. Africa—Nigeria, Gold Coast, Senegal. Tropical and subtropical Atlantic.

Polysiphonia Grev. 1824

Polysiphonia ferulacea Suhr., in J. Ag. *Spec. alg.* **2** (3), 980 (1863)

A few sterile tufts of this species have been found growing with *Bryocladia thyrsigera*.

Material. Nos. 32, 34 and 38 (spirit) (Lagos).

Distribution. Africa—Nigeria, Gold Coast, Cap Vert Is. Gulf of Mexico, warmer coasts of Europe, Indian and Pacific Oceans.

Pterosiphonia Falkenb., 1901

Pterosiphonia pennata (Roth) Falkenb., *Rhodomelaceen*, p. 263 (1901)
Polysiphonia pennata J. Ag., *Alg. mar. Médit.* p. 141 (1842)
Ceramium pennatum Roth, *Cat. Bot.* **2**, 171 (1800)

A very rare plant, growing with *Bryocladia thyrsigera* in isolated tufts.

Material. No. 70 (Lagos).

Distribution. Africa—Angola, Nigeria, Gold Coast, Senegal, Canary Is., Morocco. Mediterranean and warmer Atlantic coasts of France and Spain, Australia, New Zealand, Japan, California.

MYXOPHYCEAE

Entophysalidaceae

Entophysalis Kütz., 1843

Entophysalis conferta (Kütz.) Drouet and Daily, *Lloydia*, **11**, 79 (1948)
Dermocarpa prasina (Reinsch) Bern. et Thur., *Notes algol*. **2**, 73 (1880)

A very common epiphyte on larger algae, principally *Cladophora fascicularis*.

Material. Nos. 41, 42 (spirit, Lagos).

Distribution. Africa—South Africa (Barton), Nigeria, Morocco. North Atlantic, Baltic and North Seas. Mediterranean, Peru.

Oscillatoriaceae

Lyngbya C. Ag., 1824

Lyngbya confervoides C. Ag., *Syst. alg*. p. 73 (1924)

Common in all collections at Lagos, forming soft brown gelatinous cushions on rocks in sheltered crevices beyond the landward end of the surf zone, or on exposed rock faces in the surf zone. Common also in the intertidal region of Man o' War Bay.

Material. Nos. 49, 50, 52, 53 (spirit, Freetown), 43 (Lagos).

Distribution. Africa—Nigeria, Sierra Leone, Senegal, Cap Vert Is., Grand Desert Is., Morocco, Tangier. Cosmopolitan.

Lyngbya meneghiniana Gom., in Morot, *J. Bot., Paris*, **4**, 354 (1890)

Forms flat black disks in the same situations as *L. confervoides*. Common in all collections at Lagos. This species is more usually epiphytic in other places.

Material. No. 44 (Lagos).

Distribution. Africa—Nigeria. Tropical and subtropical around the world.

Lyngbya semiplena (Ag.) J. Ag., *Alg. mar. Med*. p. 11 (1842)

Found on sand in brackish water, Ikoyi Beach, Lagos Lagoon, and also on pebbles in the fresh-water streams running into Man o' War Bay at low tide, and on sand generally, in the intertidal region.

Material. No. 45 (Lagos), 50, 53 (spirit, Freetown).

Distribution. Africa—South Africa, Nigeria, Sierra Leone, Senegal, Tangier. Cosmopolitan.

Microcoleus Desmaz., 1823

Microcoleus chthonoplastes (Fl. Dan.) Thur., *Ann. sci. nat*. (6), *Bot*. **1**, 378 (1875)

Forms part of the greenish growth covering the sand and scoriaceous rocks in the intertidal region of Man o' War Bay.

Material. No. 52 (spirit, Freetown).

Distribution. Africa—Cameroons, Nigeria, Sierra Leone, Senegal, Cap Vert Is., Morocco. Cosmopolitan.

Skujaella G. de Toni, 1939

Skujaella thiebautii (Gom.) G. de Toni, Noterelle de nomencl. algol. IX, in *Arch. Bot.* **15**, 292 (1939)
Oscillatoria theibautii (Gom.) Geitler, in Rabenhorst's *Kryptog.-Fl.* **15**, 967 (1930–2)
Trichodesmium theibautii Gom., in Morot, *J. Bot., Paris*, **4**, 356 (1890)

This is so far the only blue-green alga to be found in plankton.

MATERIAL. Nos. 76, 80–1, 83–5 (Lagos).

DISTRIBUTION. Africa—Nigeria, Canary Is. Elsewhere widely spread in warmer waters in plankton.

Symploca Kütz., 1843

Symploca atlantica Gom., Monographie des Oscillariées, in *Ann. sci. nat. Bot.* **16**, 129 (1892)

Not uncommon on rocks in the surf zone at Lagos, generally growing with *Giffordia mitchellae*.

MATERIAL. No. 46 (Lagos).

DISTRIBUTION. Africa—Nigeria. North Atlantic coasts of Europe, West Indies, Mauritius.

BACILLARIOPHYCEAE

COSCINODISCEAE

Melosira C. Ag., 1824

Melosira granulata (Ehrenb.) Ralfs, in Pritch. *Hist. Infus.* ed. **4**, 820 (1861)

This fresh-water species was found in collections made in the Lagoon and in the harbour in June and September 1954 at both high and low tides in plankton. It was also found at the harbour entrance at low tide in the June collection. It is apparently a common species in brackish water lagoons in West Africa (Hustedt, 1910) (Zanon, 1941).

MATERIAL. Nos. 61, 63, 65, 68, 71–3 (spirit, Lagos).

DISTRIBUTION. Africa—Nigeria, Dahomey, French West Africa, Cap Vert Is., as a brackish water or marine species. Cosmopolitan in fresh-water plankton.

Melosira sulcata (Ehrenb.) Kütz., *Die kies. Bacill.* p. 55 (1844)

In plankton but very rare.

MATERIAL. No. 71 (Wilmot Point, September 1954, low tide).

DISTRIBUTION. Africa—Nigeria. Cosmopolitan.

Podosira Ehrenb., 1840

Podosira montagnei Kütz., *Die kies. Bacill.* p. 52 (1844)

Commonly epiphytic on larger algae.

MATERIAL. Nos. 21, 38, etc. (Lagos), 53 (spirit, Freetown).

DISTRIBUTION. Africa—Nigeria, Sierra Leone. Cosmopolitan.

Coscinodiscus Ehrenb., 1838

Coscinodiscus asteromphalus Ehrenb., in *S.B. preuss. Akad. Wiss.* 1844, p. 77 (1844)

In nearly half the collections and usually relatively frequent; planktonic.

MATERIAL. Nos. 60, 62, 71, 73, 75–8, 81–2, 85 (spirit, Lagos).

DISTRIBUTION. Africa—Nigeria. European waters, Atlantic coasts of North America Gulf of California.

Coscinodiscus gigas Ehrenb., in *Abh. preuss. Akad. Wiss.* 1841, p. 412 (1843)
?*Coscinodiscus guineensis* Grun., *Diatomeen von Franz Josefs-Land*, p. 76 (1884)

In plankton, rare. Reported previously from Lagos in brackish water by Grunow (loc. cit.).

MATERIAL. Nos. 80, 83, 85 (spirit, Lagos).

DISTRIBUTION. Africa—Nigeria. Sweden, but usually widely spread in warmer waters.

Coscinodiscus jonesianus (Grev.) Ostenfold, in *Dansk Bot. Ark.* **2**, (4), 13 (1915)

Commonly occurring in plankton in some quantity. Reported from Warri by Mills (1932).

MATERIAL. Nos. 60, 62–4, 67, 71, 73–4, 76–8, 80–5 (spirit, Lagos).

DISTRIBUTION. Africa—Nigeria. Cosmopolitan.

Coscinodiscus oculus-iridis Ehrenb., in *Abh. preuss. Akad. Wiss.* 1839, p. 147 (1841)

Planktonic, occurring only twice (Wilmot Point, June 1954, high tide and Lagos Lagoon, September 1954, low tide).

MATERIAL. Nos. 62, 73 (spirit, Lagos).

DISTRIBUTION. Africa—South Africa, Nigeria. Apparently cosmopolitan.

SOLENIEAE

Guinardia Peragallo, 1892

Guinardia flaccida (Castr.) Peragallo, in *Diatomiste*, **1**, 107 (1892)

In plankton but rare, occurring only once (Tarkwa Bay, September 1954, low tide).

MATERIAL. No. 67 (spirit, Lagos).

DISTRIBUTION. Africa—Nigeria. All coasts of Europe, Atlantic coast of North America, Malay Archipelago.

BIDDULPHIEAE

Triceratium Ehrenb., 1841

Triceratium favus Ehrenb., in *Abh. preuss. Akad. Wiss.* 1839, p. 159 (1841)

In plankton but rare, occurring in the harbour entrance only (June and September 1954, high and low tide). Reported from Warri by Mills (1932).

MATERIAL. Nos. 60–1, 66–7 (spirit, Lagos).

DISTRIBUTION. Africa—South Africa, Nigeria. Apparently cosmopolitan.

Biddulphia Gray, 1821

Biddulphia chinensis Grev., in *Trans. Micr. Soc. Lond.* (N.S.), **14**, 81 (1866).

Present in several plankton collections and abundant in samples with higher salinities.

MATERIAL. Nos. 60, 62, 67, 71, 76, 77, 83–5 (spirit, Lagos).

DISTRIBUTION. Africa—Nigeria. Atlantic and Northern European waters, Red Sea, Indian Ocean, Gulf of Siam, Hong Kong.

Biddulphia pulchella Gray, *Arr. Brit. Plants*, **1**, 294 (1821)

An epiphyte, commonly present on several different species of larger algae.

MATERIAL. Nos. 21, 22, 93, etc. (Lagos).

DISTRIBUTION. Africa—Nigeria, Cap Vert Is. Cosmopolitan.

TABELLARIEAE

Grammatophora Ehrenb., 1841

Grammatophora marina (Lyngb.) Kütz., *Die kies. Bacill.* 128 (1844)

Commonly epiphytic on *Bryocladia thyrsigera*, etc., in all collections.

MATERIAL. No. 31, etc. (Lagos).

DISTRIBUTION. Africa—Nigeria. Cosmopolitan.

Grammatophora undulata Ehrenb., in *S.B. preuss. Akad. Wiss.* 1841, p. 33 (1843)

A common epiphyte on *Gracilaria dentata*, etc., in all collections.

MATERIAL. Nos. 22, etc. (Lagos).

DISTRIBUTION. Africa—Nigeria. Cosmopolitan.

ACTINODISCEAE

Radiodiscus Bale, 1913

Radiodiscus hispidus (Grun.) Mills, *Index Gen. Spec. Diatoms*, p. 1382 (1934). Voigt, in *J. Indian Bot. Soc.* **30**, (1–4), 56 (1951)

Radiodiscus chaffersei Mills, in *J. Roy. micr. Soc.* **52**, 384 (1932)

In plankton but rare, occurring only once in the harbour entrance at low tide in January 1954. Apparently a widely spread but rare warm-water form.

MATERIAL. No. 75 (spirit, Lagos).

DISTRIBUTION. Africa—Nigeria. Colombo, Singapore, Haiti.

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EXPLANATION OF PLATE 54

Fig. 1. *Bryopsis stenoptera*; herbarium specimen. (× 1½.)
Fig. 2. *Bryopsis stenoptera*; distal part of frond. (× 66.)
Fig. 3. *Bachelotia fulvescens*; filaments with plurilocular sporangia. (× 112.) All photographs of this species are taken from no. 12 in the preceding list.
Fig. 4. *Bachelotia fulvescens*; a plurilocular sporangium of the tapering cylindrical type with a terminal hair. (× 370.)
Fig. 5. *Bachelotia fulvescens*; a stalked plurilocular sporangium of the ovate pointed type. (× 300.)
Fig. 6. *Ectocarpus indicus* Sond; with plurilocular sporangia. (× 120.)

A contribution to the flora of Saudi Arabia. By M. Zohary, Hebrew University, Jerusalem, Israel

(Communicated by Dr B. P. Uvarov, C.M.G., F.R.S., F.L.S.)

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The following is an enumeration of plants collected by members of the scientific staff of the Middle East Anti-Locust Unit during the years 1942–5 in Saudi Arabia, notably in the regions of Nefud, Oman and Dhofar. The collections of these plants are deposited at the Herbarium of the Hebrew University, Jerusalem. The larger of these collections is that made by Mr D. Vesey-FitzGerald, distinguished by the scientific care in collecting, by precise labelling and notes.

The other collections were brought by some members of the scientific staff of the Plant Protection Department of the former Palestine Government, at that time headed by Dr J. E. Hardy. Mr J. Kort, connected with this Department, has made a fine collection, particularly in the Nejd region.

This enumeration includes a number of species not hitherto recorded from Saudi Arabia, as well as many new distributional data within Arabia. Blatter's *Flora Arabica*,[1] Schwartz's *Flora des tropischen Arabien*[2] and Boissier's *Flora Orientalis*[3] were used as main sources of references and names adopted by them when different from those accepted here are cited as synonyms.

The names of the collectors have been abbreviated as follows: VF, Mr D. Vesey-FitzGerald; H, Dr J. E. Hardy; K, Mr J. Kort. Other abbreviation: VN, vernacular name.

The transcription of the names of localities used by the collectors has been preserved, as also numbers of specimens wherever recorded.

GNETACEAE

Ephedra alata Decne.—Blatter, 451. Southern fringes of Great Nefud, rocky outcrop (VF, 13722/2, 12. 5. 44).

GRAMINEAE

Panicum turgidum Forsk.—Schwartz, 314. Trucial Oman, Ras al Khaima (VF, 11552, 2. 3. 43, VN Thaman).

Setaria viridis (L.) Beauv.—Schwartz, 316. Dhofar, plain behind Salala, on termite mounds (VF, 12320, 26. 9. 43).

Cenchrus ciliaris L. *Pennisetum ciliare* (L.) Link—Schwartz, 318. Nejd, Jebel Ajja, sandstone (K, 8. 2. 44); Jebel Irkan, near Hail (K, February 1944).

Cenchrus pennisetiformis Steud. & Hochst.—Boiss., **5**, 448. N.E. Arabia, Manama, foothills (VF, 11620a, 12. 3. 43, grazed). Oman, El Khatt (Hadd), gullies in foothills (VF, 14. 4. 43).

Tragus racemosus (L.) All.—Schwartz, 310. Oman, Birruddi (VF, 1179, 9. 4. 43, grazed, collected and dried; VN, Feth).

Chrysopogon aucheri (Boiss.) Stapf—Schwartz, 306. Nejd, Aruma Plateau, wadi bed in stony plateau (VF, 11866f, 29. 5. 43); Jebel Salma (VF, 13544, 7. 4. 44).

Themeda quadrivalvis (L.) Kuntze—Stapf in Prain, *Fl. Trop. Afr.* **9**, 420 Dhofar, Jebel Qa'ara (VF, 12446/2, 4. 10. 43).

[1] Blatter, E., 1919–36. Flora Arabica. *Rec. Bot. Surv. India*, **8**.

[2] Schwartz, O., 1939. Flora des tropischen Arabien. *Mitt. Inst. allg. Bot. Hamb.* **10**, 1–393.

[3] Boissier, E., 1867–88. *Flora Orientalis.* 5 vols. and suppl. Genf, Basel and Lyon.

Eremopogon foveolatus (Del.) Stapf—Schwartz, 308. Trucial Oman, Abu Dhabi, stony ridges near coast (VF, 13262, 21. 2. 24).

Dichanthium annulatum (Forsk.) Stapf—Schwartz, 307. Nejd, Aruma Plateau, wadi bed in stony plateau (VF, 11866/b, 29. 5. 43).

Hyparrhenia hirta (L.) Stapf—Schwartz, 309. Nejd, Jebel Salma (VF, 13544, 7. 4. 44); Jebel Ajja (VF, 1378, 11. 5. 44).

Cymbopogon schoenanthus (L.) Spreng. *C. circinnatus* (Steud.) Hochst. ex Schwartz, 308. Oman Mts., Ham, Wadi Siqi, rubble plain and gullies in lower hill slopes (VF, 11646 c, 20. 3. 43).

Lasiurus hirsutus Boiss. *Rottboellia hirsuta* Vahl.—Schwartz, 305. Nejd, wadis (VF, 13768/1, 20. 5. 44); Khafs, near Riyadh (VF, 11840 b, 23. 5. 43, VN el Dha'a); Wadi Rumma (VF, 13590, 13. 4. 44). Trucial Oman, Adham, gullies at base of small hillocks, where silt collects together with blown sand (VF, 11710, 9. 4. 43); Ras al Khaima, sand ridges (VF, 1159, 13. 2. 43, dominant).

Phalaris minor Retz.—Blatter, 494. Trucial Oman, silty soil, moist places after rain (VF, 13158, 29. 1. 44).

Aristida adscensionis var. *festucoides* (Poir.) Henrard—Schwartz, 323. Nejd, Jebel Shammar, gravel plains and wadis (VF, 13688/1, 8. 4. 44); Riyadh, stony ground and in runnels (VF, 11832 b, 22. 5. 43). N.E. Arabia, Manama, foothills (VF, 11620 h, 12. 3. 43).

Aristida adscensionis var. *pumila* (Decne.) Coss. & Dur.—Schwartz, 323. Nejd, Jebel Hubran (H, 22. 1. 44); Hail—Taima, granite sand (K, 8. 2. 44); Oman, western Hajar Mts., silty deposits in runnels (VF, 13244, 17. 2. 44); El Khatt, gullies in foothills (VF, 11722, 17. 4. 43). Trucial Oman, Ras al Khaima, dunes of red sand (VF, 13172, 5. 2. 44).

Aristida obtusa Del.—Schwartz, 320. Nejd (VF, 13566, 11. 4. 44). Transjordan, Edom, Wadi Ythm (H, 25. 11. 42).

Aristida plumosa L.—Schwartz, 319. N.E. Arabia, Dahana, red sand (VF, 11820 b, 20. 5. 43); Qa'ara, Beisa (VF, 11762 d, 2. 5. 43). Nefud, around Adham (H. 13. 1. 44); southern fringes of Great Nefud, sand (VF, 13532, 3. 4. 44). Nejd, Jebel Shammar (VF, 13566, 2. 4. 44, dominant grass over wide area of plateau, especially where sandy); Nejd (VF, 13688/2, 8. 5. 44, VN Nussi).

Aristida ciliata Desf.—Schwartz, 319. Nefud, granite sand, around Adham (H, 13. 1. 44). Oman, western el Hajar Mts., Wadi el Gawr, lat. 25° N., long. 56 °E. (VF, 13244, 14. 2. 44).

Aristida hirtigluma Steud. ex Trin. & Rupr.—Schwartz, 320. Trucial Oman, Sila, Sabakha Mutti, soft silt (VF, 13454, 19. 3. 44).

Aristida scoparia Trin. & Rupr. *A. pungens* var. *scoparia* (Trin. & Rupr.) Boiss., **5**, 498. N. Arabia, most typical for sand dunes (H, 1942).

Stipa capensis Thunb. *S. tortilis* Desf.—Blatter, 497. Nejd, near Hail (VF, 13520, 2. 4. 44, the characteristic plant of wide areas); Hail, plain, granite sand (K, 19. 3. 45); Jebel Shammar (VF, 13566, 11. 4. 44); Nefud, Skaka area, el Athru, sand, *c*. 650 ft. (H, 12. 1. 43). N.E. Arabia, Manama, foothills (VF, 11620, 12. 3. 43, grazed, especially suitable for horses, VN Sania). Trucial Oman, Ras al Khaima, silty soil (VF, 13158, 29. 1. 44).

Avena alba Vahl. *A. barbata* Pott. ex Link—Blatter, 501. Nejd, Jebel Salma, gullies and ledges (VF, 13544, 7. 4. 44).

Asthenatherum forskalei (Vahl.) Nevski. *Danthonia forskalei* (Vahl.) R.Br.—Schwartz, 326. N.E. Arabia, Manama, red sand (VF, 11820 a, 20. 5. 43).

Cynodon dactylon (L.) Pers.—Schwartz, 326. Nejd, Khafs, near Riyadh, silty areas flooded during rains (VF, 11842, 23. 3. 43, VN Theiyal). Trucial Oman, Ras al Khaima, silty soil forming lawn-like patches (VF, 13172, 5. 2. 44).

Tetrapogon villosus Desf.—Schwartz, 328. Nejd, Hail (H, 21. 3. 43).

Pappophorum foxii Post—Post, *Fl. Syr. Palest. & Sinai*, ed. 2, **2**, 742. N.E. Arabia, Manama, foothills (VF, 12. 3. 43, grazed).

Koeleria phleoides (Vill.) Pers.—Blatter, 508. Dhofar, Jebel Qa'ara, places where cattle had been kept (VF, 12774, 31. 10. 43).

Eragrostis poaeoides Beauv. ex Roem. & Schult. *E. minor* Host—Schwartz, 334. N.E. Arabia, Manama, foothills (VF, 11620j, 12. 3. 43).

Aeluropus lagopoides (L.) Trin. ex Thw. *A. repens* (Desf.) Parl.—Schwartz, 335. N.E. Arabia, Occaire (Ukair), sandy coastal fringe (VF, 27. 12. 43).

Schismus barbatus (L.) Thell. *S. marginatus* Beauv.—Blatter, 512. Nejd, Jebel Shammar (VF, 13566, 11. 4. 44).

Cutandia dichotoma (Forsk.) Batt. & Trab. *Scleropoa dichotoma* (Forsk.) Parl.—Boiss., 5, 639. Nefud, el Athru (H, 15. 1. 43); southern edge of Great Nefud, sand hollows (VF, 13532, 3. 4. 44).

Trachynia distachya (L.) Link. *Brachypodium distachyon* (L.) Beauv.—Blatter, 516. Trucial Oman, Ras al Khaima, silty soil, moist places after rain (VF, 13158, 29. 1. 44).

CYPERACEAE

Cyperus conglomeratus Rottb.—Schwartz, 339. Nejd, near Riyadh, dunes of wet sand (VF, 11844, 24. 5. 43).

Cyperus conglomeratus var. *minor* Boeck. *C. conglomeratus* var. *effusus* (Rottb.) Boiss.—Schwartz, 340. Trucial Oman, coast, Arman, dunes of red sand (VF, 13046/4, 16. 1. 44, fleshy roots like *Panicum turgidum*). Oman, Bainuna, white sand (VF, 13436, 16. 3. 44).

Scirpus holoschoenus L.—Schwartz, 342. Nejd, Jebel Irkan, near Hail (K, 2. 44); Jebel Hamr, granite sand (K, 17. 3. 45).

JUNCACEAE

Juncus arabicus (Boiss.) Adamson. *J. maritimus* var. *arabicus* Aschers. & Buchen. ex Boiss.—Blatter, 468. N.E. Arabia, Manama, rocky wadi in foothills (VF, 11578c, 10. 3. 43, used in making mats); Occaire (Ukair), sandy coastal fringe (VF, 27. 12. 43).

LILIACEAE

Colchicum ritchii R.Br.—Boiss., 5, 163. Nejd, Wadi Hail, wadi beds, soft sand and stones (K, 15. 1. 45); Jebel Misma and Jebel Hubran (H, 20. 1. 44).

Gagea reticulata (Pall.) J. A. & J. H. Schult.—Boiss., 5, 208. Nejd, Hail, between stones on soft sand (K, 20. 1. 45).

Gagea tenuifolia (Boiss.) Fomin. *G. reticulata* var. *tenuifolia* Boiss.-Blatter, 459. N.E. Arabia, Birket al Ashar (H, 28. 1. 43).

Asphodelus tenuifolius Cav.—Schwartz, 349. Nejd, Hail—Taima, granite sand (K, 8. 2. 44). Trucial Oman, Ras al Khaima (VF, 1154c, 11. 2. 43, VN Kawthar).

Asphodelus viscidulus Boiss.—Blatter, 462. Nejd, sand patches in gravel plain (VF, 13514, 1. 4. 44).

URTICACEAE

Forsskalea tenacissima L.—Schwartz, 28. Nejd, Jebel Salma (VF, 13544, 7. 4. 44); Hail (K, 13. 1. 43); Jebel Hamr, between rocks (K, 17. 3. 45).

POLYGONACEAE

Calligonum comosum L'Hérit.—Schwartz, 33. N.E. Arabia, Birket al Ashar, 650 ft. (H, 20. 1. 43, VN Arta). Trucial Oman, Ras al Khaima, sandy escarpment (VF, 11512, 13. 11. 43).

Pteropyrum scoparium Jaub. & Spach—Schwartz, 33. Oman, Batina, Wadi Ham, Kulba, plain of stony detritus (VF, 11644d, 20. 3. 43).

Emex spinosa (L.) Campd.—Schwartz, 31. Nejd, Hail-Taima (K, 8. 2. 44). Trucial Oman, Ras al Khaima, hollows in sand dunes (VF, 1154a, 11. 2. 43).

Rumex vesicarius L.—Schwartz, 32. N.E. Arabia, Dahana, rocky hillsides (VF, 10. 3. 43, used as salads); Manama, rocky hillsides (VF, 10. 3. 43).

CHENOPODIACEAE

Chenopodium murale L.—Schwartz, 34. Nejd, Jebel Salma (VF, 13544, 7. 4. 44). Trucial Oman, Ras al Khaima, moist places after rain (VF, 13158, 29. 1. 44).

Atriplex tatarica L.—Boiss., 4, 910. Trucial Oman, Ras al Khaima, silty soil (VF, 13172, 5. 2. 44).

Atriplex leucoclada Boiss. *Obione leucoclada* (Boiss.) Ulbr.—Schwartz, 35. Nefud, el Defafat (edge of Nefud), mud flat (K, 22. 1. 44, VN Rukhal).

Atriplex halimus L.—Blatter, 404. N. Arabia, salty ground (H, 1942).

Atriplex farinosa Forsk.—Schwartz, 35. Dhofar, coastal belt, low sand dunes (VF, 12820, 3. 11. 43).

Halocnemum strobilaceum (Pall.) Bieb.—Blatter, 407. Trucial Oman, Abu Dhabi, sea coast, salt flat (VF, 13262/2, 22. 2. 44).

Halopeplis perfoliata (Forsk.) Bunge ex Aschers. & Schweinf.—Schwartz, 36. Trucial Oman, Abu Dhabi, sea coast, salty flat (VF, 13261/1, 22. 2. 44).

Suaeda vermiculata Forsk.—Schwartz, 37. N.E. Arabia, Sikuk, near Selwa, muddy salty hollow (VF, 12972, 31. 12. 43). N.W. Arabia, Mughaira area, salines (H, 25. 12. 43).

Suaeda aegyptiaca (Hasselq.) Zohary, comb.nov. *Chenopodium aegyptiacum* Hasselq., *It. Palaest.*, 460 (1757). *S. baccata* Forsk.—Schwartz, 36. E. Saudi Arabia, Mintur, salt flat (VF, 1294, 7. 12. 43). Oman, Batina coast, Suwaik (VF, 13220, 12. 2. 44, forming large bushes on waste land and in cultivation near the sea).

Bienertia cycloptera Bunge ex Boiss., **4**, 945. E. Saudi Arabia, Mintur, salt flat (VF, 1294, 4. 12. 43).

Haloxylon persicum Bunge ex Boiss. & Buhse. *H. ammodendron* sensu Boiss., **4**, 948, p.p. Nejd, Tebuk, 755 ft. (H, 19. 12. 42). Oman, Buraimi (Bareimi?), sand hummocks in beds of wadis penetrating dunes (VF, 13350, 29. 2. 44, shrub 12 ft. high).

Haloxylon salicornicum (Moq.) Bunge ex Boiss. *H. schweinfurthii* Aschers.—Blatter, 411. Nejd, el M'Kuttaba, sand, about 650 ft. (H, 31. 12. 42, abundant in sandy Hammada). Trucial Oman, Ras al Khaima, salty soil (VF, 13172, 5. 2. 44, codominant plant, VN Rimth). S. Iraq, between Basra and Tel al Lahm, flat gravel plain (VF, 12874, 29. 11. 43).

Seidlitzia rosmarinus Bunge ex Boiss.—Blatter, 410. S.E. Transjordan, Tebuk area, Bir Ibn Hirmas, salty ground, *c.* 750 ft. (H, 18. 12. 42).

Salsola tetrandra Forsk.—Blatter, 413. Trucial Oman, Sabakha Mutti, pebbly ground (VF, 13020, 4. 1. 44). Specimen very hirsute, Dhofar, Jebel Qa'ara, mountain descent in wadi bed (VF, 12772, 30. 10. 43). (Our specimen has pentamerous flowers and belongs therefore to the typical form (*S. tetragona* Del.); its fruits also have developed wings typical of the *tetragona* form; the perigonium is glabrous.)

Anabasis articulata (Forsk.) Moq.—Blatter, 413. S.E. Transjordan, Wadi Ythm (H, 28. 11. 42, VN Ajram).

Anabasis setifera Moq.—Blatter, 414. N.E. Arabia, Occaire (Ukair), hard ground of escarpment where sand and gravel are mixed (VF, 12958, 28. 12. 43).

Agathophora alopecuroides (Del.) Bunge—Blatter, 410. N. Arabia, stony desert (H, spring 1942).

AMARANTHACEAE

Aerva javanica (Burm. f.) Juss. ex Schult.—Schwartz, 43. Nejd, Jebel Salma (VF, 13544, 7. 4. 44); Jebel Irkan, rocky ground, scattered between cracks and rocks (K, February 1944). N.E. Arabia, Manama, rocky hillock (VF, 11578, 10. 3. 43, VN 'Ara, used for stuffing pillows). Dhofar, Jebel Qa'ara (VF, 12746, 24. 10. 43).

AIZOACEAE

Mesembryanthemum forskahlei Hochst. ex Boiss.—Blatter, 207. E. Nejd, Besaita, sand, 540 ft. (H, 31. 12. 42, VN Samh).

Aizoon hispanicum L.—Blatter, 208. Nejd (VF, 13584, 13. 4. 44); Jebel Salma (VF, 13544, 7. 4. 44); Hail-Taima, granite sand (K, 8. 2. 44). N.E. Arabia, Manama, foothills (VF, 12. 3. 43, VN Kfalray, grazed).

CARYOPHYLLACEAE

Spergula fallax (Lowe) E. H. L. Krause. *S. flaccida* Aschers.—Schwartz, 55. Nejd, Jebel Salma (VF, 13544, 7. 4. 44); Hail-Taima, granite sand (K, 8. 2. 44). Trucial Oman, Ras al Khaima, silty soil (VF, 13158, 29. 1. 44). N.E. Arabia, Manama, foothills (VF, 11620g, 12. 3. 43, VN Agash, grazed).

Robbairea delileana Milne-Redh. *Polycarpaea prostrata* sensu Schwartz, 55. Oman, Birruddi (VF, 117g, 9. 4. 43).

Polycarpaea repens (Forsk.) Aschers. & Schweinf.—Schwartz, 54. Nefud, Skaka, sand dunes (H, 6. 1. 43); southern fringes of Great Nefud (VF, 13530, 3. 4. 44). Nejd, sands and gravel plains (VF, 13514, 1. 4. 44); El Defafat, edge of mud plain (H, 22. 1. 44); Jebel Shammar (H, 4. 3. 43). N.E. Arabia, Dahana, red sand (VF, 11822b, 13468, 20. 5. 43).

Herniaria hemistemon Gay—Blatter, 393. Nefud, Skaka, sand dunes (K, 6. 1. 43).

Paronychia arabica (L.) Del.—Schwartz, 53. N.W. Arabia, Qassani (Bassaita), 540 ft., sandy soil (H, 29. 12. 42).

Paronychia desertorum Boiss. *P. lenticulata* Aschers. & Schweinf.—Schwartz, 53. Nejd, Jebel Salma (VF, 13544, 7. 1. 44).

Gymnocarpos decandrus Forsk.—Blatter, 393. Nejd, Jebel Ajja, sandstone (K, 8. 2. 44). Trucial Oman, Batina, Wadi Ham, Kulba, plain of stony detritus (VF, 11644c, 20. 3. 43). N.E. Arabia, Manama, silt, foothills (VF, 1166, 10. 3. 43, grazed).

Sclerocephalus arabicus Boiss.—Schwartz, 53. Nejd, Riyadh, stony ground (VF, 11828, 20. 4. 43). N.E. Arabia, Beisa, Qa'ara (VF, 11762, 2. 5. 43); Dahana, sand belt (VF, 20. 5. 43). Oman Mts., Ham, Wadi Siqi, rubble plains in mountains (VF, 11646, 20. 3. 43).

Cometes surattensis L.—Schwartz, 53. Oman, El Khatt, ledges in foothills (VF, 11722, 14. 4. 43).

Cometes abyssinica R.Br.—Schwartz, 54. N.E. Arabia, Manama, foothills (VF, 11620g, 12. 3. 43, VN Hammad, grazed, used as salad).

Gypsophila viscosa Murr.—Boiss., 1, 551. Southern fringes of Great Nefud, sandy hollows (VF, 13532, 30. 4. 44).

Silene conoidea L.—Blatter, 61. Jebel Irkan, S. of Hail, red granite sand (K, 31. 12. 43).

Silene villosa Forsk.—Blatter, 63. Southern fringes of Great Nefud, sandy hollows (VF, 13532, 3. 4. 44). Trucial Oman, Ras al Khaima (VF, 15. 3. 43).

Silene arabica Boiss. *S. affinis* Boiss. non Godr.—Blatter, 60. Nejd, Hail, rocks and soft sand (K, 1. 2. 45, VN Tarba). N.W. Arabia, Qassani (H, 28. 12. 42).

Silene colorata Poir.—Schwartz, 57. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

Silene arenosa C. Koch. *S. linearis* Decne. non Sweet—Blatter, 62. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

PAPAVERACEAE

Papaver polytrichum Boiss. & Kotschy—Boiss., 1, 113. Nejd, Jebel Ajja, S.W. of Hail (K, 13. 3. 45).

Fumaria parviflora Lam.—Schwartz, 61. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

CAPPARIDACEAE

Cleome arabica L.—Schwartz, 64. Edge of Nefud, el Defafat, mud flat (K, 22. 1. 44).

Cleome trinervia Fres.—Schwartz, 64. Oman Mts., Ham, Wadi Siqi (VF, 11646h, 20. 3. 43).

Capparis decidua (Forsk.) Edgew.—Schwartz, 66. E. Nejd, Wadi Kheibar, edge of wadi (K, 20. 2. 44).

Capparis cartilaginea Decne. *C. galeata* Fres.—Schwartz, 66. Dhofar, descent of mountain, in wadi (VF, 12772, 30. 4. 43).

CRUCIFERAE

Morettia canescens Boiss.—Blatter, 13. Nejd, Wadi Izheia, stones and granite sand (K, 6. 2. 45).

Morettia parviflora Boiss.—Schwartz, 74. Oman, western el Hajar Mountains, Wadi el Gawr (VF, 13244, 17. 2. 44).

Matthiola arabica Boiss.—Blatter, 10. Nefud, sands (K, 31. 1. 44); southern fringes of Great Nefud, Hail (VF, 13530, 3. 4. 44); El Defafat, S.W. edge of Nefud (K, 22. 1. 44). Nejd, Jebel Ajja, sandstone (K, 8. 2. 44).

Matthiola longipetala (Vent.) DC. *M. oxyceras* DC.—Blatter, 11. Nefud, Skaka, sand dunes (H, 28. 1. 42). Nejd, Jebel Salma (VF, 13544, 7. 4. 44); Hail, rocks and soft sand (K, 1. 2. 45, VN Shikar); S. of Hail, granite sand (K, 31. 12. 43).

Eremobium lineare (Del.) Boiss. *Malcolmia aegyptiaca* sensu Schwartz, 74. Nefud, around Adham (H, 13. 1. 44); southern fringes of Great Nefud, Hail, sandy hollows (VF, 13532, 3. 4. 44). Nejd, S. of Hail, firm red granite sand (K, 31. 12. 43); Nejd, Qasum, sand patches on gravel plain (VF, 13514, 1. 4. 44). Trucial Oman, Abu Dhabi, white sand dunes (VF, 13324, 26. 2. 44). Oman, Bainuna, white sand (VF, 13435, 16. 3. 44).

Farsetia longisiliqua Decne.—Schwartz, 73. N.E. Arabia, Dahana, sand belt (VF, 13468, 28. 3. 44).

Sisymbrium erysimoides Desf.—Schwartz, 74. Nejd, Jebel Salma (VF, 13544, 7.4.44). Trucial Oman, Ras al Khaima, moist places after rain (VF, 13158, 29. 1. 44).

Notoceras bicorne (Ait.) Amo. *N. canariense* R.Br.—Schwartz, 73. Nejd, Hail-Taima, on hard granite sand soil (K, 8. 2. 44). Oman Mts., Ham, Wadi Siqi, rubble plains in the mountains (VF, 11646c, 20. 3. 43).

Anastatica hierochuntica L.—Schwartz, 73. Nejd, pebbly plain (VF, 13520, 2. 4. 44). N.W. Arabia, Bseita (Bassaita?), 540 ft. (H, 27. 12. 42).

Lepidium aucheri Boiss.—Blatter, 27. Nejd, Hail-Taima, granite sand (K, 8. 2. 44).

Erucaria lineariloba Boiss.—Boiss., 1, 366. Nefud, around Adham (H, 13. 1. 44). Trucial Oman, Ras al Khaima, silty soil, moist after rain (VF, 13158, 29. 1. 44). N.E. Arabia, Manama, foothills (VF, 11572, 9. 3. 43).

Isatis aleppica Scop.—Blatter, 30. Nejd, Jebel Salma (VF, 13544, 7. 4. 44, one of the characteristic plants); Jebel Ajja, S.W. of Hail (K, 13. 3. 45).

Schimpera arabica Steud. & Hochst.—Blatter, 31. Nejd, Hail-Taima, granite sand (K, 8. 2. 44). N.E. Arabia, Birket al Ashar (H, 21. 1. 43); Jebel Hubran (H, 20. 1. 44).

Diplotaxis acris (Forsk.) Boiss.—Schwartz, 70. Nejd, Hail (H, 20. 1. 43); Jebel Salma (VF, 13544, 7. 4. 44).

Brassica tournefortii Gouan—Blatter, 22. N.E. Arabia, Manama, foothills, silt and sand, usually near bushy vegetation (VF, 11578b, 10. 3. 43).

Savignya parviflora (Del.) Webb. *S. aegyptiaca* DC.—Blatter, 24. Nefud, Skaka (H, 16. 3. 43); Jauf (31. 12. 42). Trucial Oman, Sabakha Mutti, Ain Ba'aja (VF, 19. 3. 44).

Zilla spinosa (Turra) Prantl—Blatter, 31. Hejaz, Tebuk area, sand fields and wadis, 775 ft. (H, 27. 12. 42). Nejd, Aruma Plateau, wadi bed (VF, 11866i, 29. 5. 43); near

Riyadh (VF, 11863c, 22. 5. 43); Hail-Taima, granite sand (K, 8. 2. 43); Jebel Ajja, S.W. of Hail, water flow between rocks (K, 1. 2. 45). Oman, Bareimi (Buraima?), sands and wadis (VF, 13354, 28. 2. 44).

RESEDACEAE

Ochradenus baccatus Del.—Schwartz, 75. Nejd, Jebel Ajja, S.W. of Hail, sandstone (K, 8. 2. 44).

Oligomeris linifolia (Vahl.) J. F. Macbr. *O. subulata* Webb—Schwartz, 75. Oman Mts., Ham, Wadi Siqi (VF, 20. 3. 43); Bainuna (VF, 13441, 16. 3. 44).

Caylusea hexagyna (Forsk.) M. L. Green. *C. canescens* St.-Hil.—Schwartz, 77. Hejaz, Tebuk area, about 750 ft. (H, 19. 12. 42). Nejd, Aruma Plateau (VF, 11866j, 29. 5. 43); Jebel Salma (VF, 13544, 7. 4. 44).

MORINGACEAE

Moringa peregrina (Forsk.) Fiori. *M. aptera* Gaertn.—Schwartz, 78. Dhofar, Risut, a characteristic shrub of wadi beds (VF, without date).

ROSACEAE

Neurada procumbens L.—Schwartz, 82. Nejd, Skaka, sand dunes (H, 13. 1. 43, VN Saadan). N.E. Arabia, Dahana, sand belt (VF, 13468, 28. 3. 44, one of the characteristic plants here). Southern fringes of Great Nefud (VF, 13530, 3. 4. 44).

LEGUMINOSAE

Trigonella stellata Forsk.—Blatter, 131. Nejd, Jebel Salma (VF, 13544, 7. 4. 44). N.E. Arabia, Manama, foothills (VF, 11620b, 12. 3. 43, VN Shurshur, grazed).

Medicago laciniata var. *brachyacantha* Boiss. *M. aschersoniana* Urb.—Blatter, 133. Trucial Oman, Ras al Khaima, in hollows of sand dunes after rain (VF, 1154d, 11.2.43). Also collected in Jebel Salma and Dahana.

Lotus halophilus Boiss. & Sprunn. *L. villosus* Forsk. non Burm. f.—Blatter, 141. Trucial Oman, Ras al Khaima (VF, February 43).

Hippocrepis bicontorta Lois.—Blatter, 161. Nejd, Hail, sandstone, about 750 ft. (H, 28. 1. 43). Trucial Oman, Ras al Khaima, white sand of coastal belt (VF, 13164, 29. 1. 44), ibid., red sand at al Kharan (VF, 13172, 5. 2. 44).

Astragalus tribuloides Del.—Blatter, 160. Nejd, Hail-Taima, granite sand (K, 8.2.44).

Astragalus hauarensis Boiss. *A. gyzensis* Del. ex Bunge p.p.—Blatter, 157. Nejd, sand patches on gravel plain (VF, 13514, 1. 4. 44).

Astragalus spinosus (Forsk.) Muschl.—Blatter, 159. El Defafat, edge of Nefud (H, 22. 1. 44). Nejd, Hail, about 750 ft. (H, 27. 1. 43).

Astragalus kahiricus DC.—Blatter, 155 (err. *cahiricus*). Nejd, Hail, sandy rock (H, 27. 1. 43).

GERANIACEAE

Erodium moschatum subsp. *deserti* Eig in *Beih. bot. Zbl.* **50** (2), 236 (1932). Nejd, Jebel Ajja, S.W. of Hail (K, 13. 3. 45). Trucial Oman, Ras al Khaima, silty soil moist after rain (VF, 13158, 29. 1. 44).

Erodium triangulare (Forsk.) Muschl.—Blatter, 105. Nejd, Hail area, al Athru, sand (H, 6. 1. 43); Hail-Taima, hard granite sand (K, 8. 2. 44).

Erodium glaucophyllum (L.) L'Hérit.—Blatter, 104. N.W. Arabia, Qassani (Bassaita), sandy soil (H, 29. 12. 42).

Monsonia nivea (Decne.) Decne. ex Webb—Blatter, 101. Southern fringes of Great Nefud, sandy hills (VF, 13532, 3. 4. 44). Oman, Bainuna (VF, 13440, 16. 3. 44).

ZYGOPHYLLACEAE

Tribulus macropterus Boiss.—Schwartz, 123. Oman, Bainuna, white sand (VF, 13440, 16. 3. 44).

Fagonia bruguieri DC.—Schwartz, 120. N.E. Arabia, Beisa, Qa'ara (VF, 11762b, 2. 5. 43).

Zygophyllum simplex L.—Schwartz, 122. Trucial Oman, Abu Dhabi, stony and silty places near coast (VF). Dhofar, Risut (?), gravel bed of wadi near the sea and above on coastal rocks (VF).

Zygophyllum coccineum L.—Schwartz, 122. Oman, Sharta, white sand not far from sea (VF, 1328, 7. 2. 44, VN Harm); Batina coast, Suwaik, salty waste land near sea (VF, 13220, 12. 2. 44).

RUTACEAE

Haplophyllum propinquum Spach. *Ruta propinqua* (Spach) Schwartz, 125. Nejd, Aruma Plateau, wadi bed (VF, 11866, 29. 5. 43).

EUPHORBIACEAE

Euphorbia isthmia Täckh. in *Svensk Bot. Tidskr.* **26**, 374 (1932). Nejd, Jebel Shammar, wadis (VF, 13690/3, 8. 5. 44).

Euphorbia granulata Forsk.—Schwartz, 143. Nejd, Khafs, near Riyadh, thin layer of sand overlying fine silt (VF, 23. 5. 43); Hail-Taima, granite sand (K, 8. 2. 44).

Euphorbia retusa Forsk. *E. cornuta* Pers.—Blatter, 425. Nejd, Khafs, near Riyadh, depression where silt accumulates (VF, 11842b, 23. 5. 43).

Euphorbia peplus L.—Schwartz, 146. Nejd, Hail (H, 23. 1. 43).

ANACARDIACEAE

Rhus tripartita (Ucria) Fiori, *Nuov. Fl. Anal. Ital.* **2**, 119 (1925). Nejd, Hail district, Jebel Irkan (K, 15. 1. 45); Jebel Shammar (4. 2. 43).

RHAMNACEAE

Ziziphus nummularia (Burm. f.) Wight & Arn.—Boiss., **2**, 13. Luqa area, depression (H, 18. 1. 43). A branch with pubescent leaves has been collected near Hail on Jebel Irkan (K, February 1944), perhaps a variety of *Z. lotus*.

MALVACEAE

Malva aegyptia L.—Blatter, 76 (err. *aegyptiaca*). Edge of Nefud, el Defafat, mud flat (H, 22. 2. 44).

Malva parviflora L.—Schwartz, 160. Nejd, Jebel Salma (VF, 13544, 7. 4. 44); Hail-Taima, granite sand (K, 8. 2. 44). Trucial Oman, Ras al Khaima, moist places after rain (VF, 13158, 29. 1. 44).

STERCULIACEAE

Glossostemon bruguieri Desf.—Schwartz, 167. Nejd, Jebel Salma, where wadis flowed into plain (VF, 13544, 7. 4. 44).

TAMARICACEAE

Tamarix orientalis Forsk. *T. articulata* Vahl.—Schwartz, 169. Oman, Wadi Ylyyly, bed of wadi (VF, 13136, 25. 1. 44, VN Ethel).

Tamarix macrocarpa (Ehrenb.) Ehrenb. ex Bunge—Blatter, 73. Trucial Oman, Ras al Khaima, estuary near sea (VF, 11522, 20. 2. 43).

CISTACEAE

Helianthemum ledifolium (L.) Mill.—Blatter, 50. Nejd, Jebel Irkan, S.W. of Hail, rocks and soft sand (K, 1. 2. 45).

Helianthemum kahiricum Del.—Blatter, 50. N.E. Saudi Arabia, Birket al Ashar (H, 28. 1. 43).

Helianthemum lippii (L.) Pers.—Schwartz, 170. Edge of Nefud, el Defafat (H, 22. 1. 44). Nejd, Jebel Salma (VF, 13544, 7. 4. 44). N.E. Arabia, Dahana, sand belt (VF, 13468, 20. 3. 44). Oman, western el Hajar Mts., Wadi el Gawr (VF, 13244, 17. 2. 44). Trucial Oman, Ras al Khaima, white sand of coastal belt (VF, 13164, 29. 1. 44).

UMBELLIFERAE

Pimpinella barbata (DC.) Boiss.—Boiss., 2, 867. Oman, El Khatt, gullies in foothills (VF, 11722, 14. 4. 43).

Pimpinella puberula (DC.) Boiss.—Boiss., 2, 866. Trucial Oman (VF, 1174, 8. 4. 43).

Ducrosia anethifolia (DC.) Boiss.—Boiss., 2, 1036. Nejd, Khafs, near Riyadh (VF, 11840e, 23. 5. 43).

PRIMULACEAE

Anagallis arvensis subsp. *foemina* (Mill.) Schinz & Thell. *A. arvensis* var. *caerulea* Gren. & Godr.—Schwartz, 180. Nejd, Jebel Ajja, S.W. of Hail (VF, without date). Oman Mts., Ham, Wadi Siqi (VF, 30. 3. 43).

Anagallis arvensis subsp. *latifolia* (L.) Braun-Blanq. & Maire. *A. arvensis* var. *latifolia* (L.) Lange—Schwartz, 180. Nejd, Hail area (H, 23. 1. 43).

GENTIANACEAE

Centaurium pulchellum (Sw.) Druce. *Erythraea ramosissima* (Vill.) Pers.—Schwartz, 185. Dhofar, Jebel Qa'ara, water-shed zone amongst grasses (VF, 1246/9, 2. 10. 43).

APOCYNACEAE

Rhazya stricta Decne.—Schwartz, 186. N.E. Arabia, Manama, near wadis (VF, 11574, 10. 3. 43, VN Harmal, infusion of leaves used against fever).

ASCLEPIADACEAE

Periploca aphylla Decne.—Schwartz, 187. Nejd, Jebel Hamr, between rocks (K, 17. 3. 45).

Pergularia tomentosa L.—Schwartz, 195. Nejd, Jebel Ajja, sandstone (K, February 1944).

CONVOLVULACEAE

Cressa cretica L.—Schwartz, 197. N.E. Arabia, Occaire (Ukair), sands of coastal fringe (VF, 12950, 27. 12. 43).

BORAGINACEAE

Heliotropium ramosissimum (Lehm.) Sieber ex DC.—B. L. Burtt in *Kew Bull.* 1949, 138. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

Heliotropium kotschyi (Bunge) Gürke. *H. tuberculosum* (Boiss.) Boiss., 4, 147. N.E. Arabia, Occaire (Ukair), sand and gravel mixed (VF, 12958, 28. 12. 43).

Anchusa milleri Willd.—Blatter, 317. Nejd, Jebel Ajja, S.W. of Hail, between rocks (K, 13. 3. 45); Jebel Irkan, near Hail (K, February 1944); Jebel Salma, moist place (VF, 13544, 7. 4. 44).

Arnebia decumbens (Vent.) Coss. & Kral. *A. cornuta* (Ledeb.) Fisch. & Mey.—Blatter, 319. Nejd, Hail-Taima, granite sand (K, 20. 2. 44). Oman, Ham, Wadi Siqi, rubble plains in mountains (VF, 11646 d, 30. 3. 43).

Arnebia linearifolia DC.—Blatter, 320. Nefud, Skaka, sand dunes (K, 23. 3. 43).

Arnebia hispidissima (Lehm.) DC.—Schwartz, 214. Oman Mts., Bainuna (VF, 13440, 16. 3. 44).

Moltkiopsis ciliata (Forsk.) I. M. Johnston. *Lithospermum callosum* Vahl.—Schwartz, 213. Southern edge of Great Nefud, sand dunes (VF, 3. 4. 44). N.E. Arabia, Beisa, Qa'ara (VF, 2. 5. 43); Dahana, red sand (VF, 20. 5. 43). Trucial Oman, Ras al Khaima (VF, 2. 3. 43).

Sericostoma persicum (Burm. f.) B. L. Burtt. *Lithospermum kotschyi* Boiss. & Hohen.—Boiss., **4**, 219. Trucial Oman, Ras al Khaima, Gezira, white coastal sands (VF, 13164, 29. 1. 44).

Paracaryum boissieri Schweinf. in *Mém. Inst. Égypt.* **2**, 768 (1889). Nejd, Hail-Taima, granite sand (K, 20. 2. 44).

Trichodesma africanum (L.) Lehm.—Schwartz, 211. Nejd, Jebel Ajja, S.W. of Hail, sandstone; Jebel Irkan, near Hail (K, February 1944); Jebel Salma (VF, 13544, 7. 4. 44).

VERBENACEAE

Phyla nodiflora (L.) Greene. *Lippia nodiflora* (L.) Michx.—Schwartz, 216. Dhofar, foothills, moist places around spring (VF, 1236/6, 25. 9. 43).

LABIATAE

Lavandula pubescens Decne.—Schwartz, 220. Nejd, Jebel Salma (VF, 13544, 7.4.44); Jebel Misma (H, 20. 1. 44).

Salvia lanigera Poir. *S. controversa* Ten.—Blatter, 375. Nejd, Jebel Shammar, Lukita, sandstone (H, 5. 2. 43).

Teucrium oliveranum Ging. ex Benth.—Blatter, 383. Nejd, S.W. of Hail (K, 10. 4. 45).

Teucrium polium L.—Schwartz, 218. Southern fringes of Great Nefud, rocky outcrops in sand (VF, 13722/1, 12. 5. 44). Nejd, Jebel Salma (VF, 13544, 7. 4. 44); near Riyadh (VF, 11838, 23. 5. 43, VN Ja'ad); Aruma Plateau, wadi bed (VF, 11866 b, 29. 5. 43).

SOLANACEAE

Hyoscyamus pusillus L.—Schwartz, 233. Nejd, Hail-Taima, granite sand (K, 20.2.44).

Lycium persicum Miers. *L. arabicum* Schweinf. ex Boiss.—Schwartz, 233. Trucial Oman, Ras al Khaima (VF, 11510, March 1943).

SCROPHULARIACEAE

Linaria acerbiana Boiss. **4**, 366. Nejd, Hail (K, 23. 1. 43).

Linaria haelava (Forsk.) Del.—Blatter, 342. Nejd, Jebel Irkan, S.W. of Hail, amongst rocks and soft sand (K, 1. 2. 43).

Misopates orontium (L.) Raf. *Antirrhinum orontium* L.—Schwartz, 242. Nejd, Hail (K, 23. 1. 43).

ACANTHACEAE

Blepharis ciliaris (L.) B. L. Burtt. *B. edulis* (Forsk.) Pers.—Schwartz, 253. Nejd, Riyadh, stony places (VF, 11860, 28. 5. 43).

PLANTAGINACEAE

Plantago cylindrica Forsk.—Blatter, 386. N.E. Arabia, Qa'ara, Beisa, especially sandy plains (VF, 11760, 2. 5. 43, characteristic herb of the area). Southern fringes of Great Nefud (VF, 13532, 3. 4. 44). N.E. Arabia, Dahana, sand belt (VF, 13468, 28. 3. 44).

Plantago amplexicaulis Cav.—Blatter, 385. Nejd, Jebel Salma (VF, 13544, 7. 4. 44). N.E. Arabia, Manama, foothills (VF, 11620d, 12. 3. 43, grazed, famine food, VN Jenam).

Plantago ovata Forsk.—Schwartz, 260. Nefud, sandy rock, about 700 ft. (H, 4. 1. 42). Trucial Oman, Ras al Khaima, silty soil (VF, 13158, 29. 1. 44).

Plantago ciliata Desf.—Schwartz, 260. Nejd, plains (H, 2. 4. 44); Hail-Taima, granite sand (K, 8. 2. 44).

Plantago afra L. *P. psyllium* L. (1762 non 1753)—Blatter, 388. N.E. Arabia, Manama, foothills (VF, 11620c, 12. 3. 43).

RUBIACEAE

Gaillonia aucheri (Guillem.) Jaub. & Spach—Schwartz, 263. Oman, Batina, Wadi Ham, Kulba, plain of stony detritus (VF, 11644b, 20. 3. 43).

Galium setaceum var. *longipedicellatum* Post—Post, *Fl. Syr. Palest. & Sinai*, ed. 2, 1, 599. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

Galium tricornectum Dandy. *G. tricorne* Stokes pp.—Blatter, 225. Trucial Oman, Ras al Khaima, in shelter of thickets (VF, 13172, 5. 2. 44).

Callipeltis aperta Boiss. & Buhse—Blatter, 223. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

DIPSACACEAE

Scabiosa aucheri Boiss.—Blatter, 228. Nejd, Jebel Shammar, on sand blown over rocky hills and sandy plateau (VF, 13566, 11. 4. 44).

CUCURBITACEAE

Colocynthis vulgaris Schrad. *Citrullus colocynthis* (L.) Schrad.—Schwartz, 267. Nejd, Wadi M'Kattaba (H, 28. 12. 43, VN Handal); near Riyadh, thin sand overlying silt (VF, 11840c, 23. 5. 43).

Cucumis prophetarum L.—Schwartz, 268. S. Transjordan, Wadi Ythm (H, 14. 12. 42).

COMPOSITAE

Asteriscus pygmaeus (DC.) Coss. & Dur. *Odontospermum pygmaeum* (DC.) Benth. & Hook. ex Aschers. & Schweinf.—Blatter, 249. Nejd, silty soil (VF, 13514, 1. 4. 44). N.E. Arabia, Dahana, sand belt (VF, 13468, 28. 3. 44).

Asteriscus graveolens (Forsk.) Less. *Odontospermum graveolens* (Forsk.) Schultz Bip.—Blatter, 249. Edge of Nefud, el Defafat, mud flat (H, 22. 1. 44, VN Naked). N.W. Arabia, Mughaira, southern part of W. Sirhan (K, January 1944).

Anvillea garcinii (Burm. f.) DC.—Blatter, 249. Nejd, Jebel Salma (VF, 13544, 7.4.44, one of the most conspicuous plants of the mountain gullies); near Riyadh (VF, 11836b, 22. 5. 43, VN Nuqd); Aruma Plateau (VF, 11866a, 29. 5. 43). N.E. Arabia, Birket al Ashar (H, 20. 1. 43).

Pulicaria glaucescens (Boiss.) Jaub. & Spach—Boiss., 3, 209. N.E. Arabia, Manama, foothills (VF, 11615, 10. 3. 43, produces a yellow dye).

Pulicaria undulata (L.) C. A. Mey.—Schwartz, 283. Nejd, Jebel Hamr, between rocks (K, 17. 3. 45).

Pulicaria crispa (Forsk.) Oliv.—Schwartz, 283. N.W. Arabia, Mughaira, southern part of Wadi Sirhan (H, 23. 3. 43, VN Yreiba). Nejd, Riyadh, runnels in stony country (VF, 11832a, 22. 5. 43). Nefud, el Defafat, mud flat, edge of Nefud (H, 12. 1. 44). Trucial Oman, Ras al Khaima, silty soil (VF, 13158, 29. 1. 44).

Rhanterium epapposum Oliv.—Blatter, 248. Trucial Oman, Adham, gullies at base of small hillocks where silt is collected with blown sand (VF, 11710, 9. 4. 43, VN Arfaj, grazed, camel fodder).

Gymnarrhena micrantha Desf.—Blatter, 248. N.E. Arabia, Dahana, sand belt (VF, 13468, 28. 4. 44). Nejd, shallow silt basins (VF, 13514, 1. 4. 44).

Filago spathulata var. *prostrata* Boiss.—Blatter, 237. Nejd, shallow silt bottom (VF, 13514, 1. 4. 44).

Ifloga spicata (Forsk.) Schultz Bip.—Schwartz, 277. N.W. Arabia, Qassani (Bassaita), sand fields, 540 ft. (H, 29. 12. 42).

Achillea fragrantissima (Forsk.) Schultz Bip.—Blatter, 252. N.W. Arabia, Mughaira, southern edge of Wadi Sirhan (K, January 1944, VN Kayssun). Nejd, Aruma Plateau, wadi bed through stony plateau (VF, 11866k, 29. 5. 43); near Riyadh (VF, 11836c, 22. 5. 43).

Matricaria aurea (Loefl.) Schultz Bip.—Blatter, 255. Trucial Oman, Ras al Khaima, silty soil (VF, 13172, 5. 2. 24).

Matricaria auriculata (Boiss.) Ball—Blatter, 255. Nejd, el Salma, silty hollows in mountains (VF, 13544, 7. 4. 44).

Artemisia monosperma Del.—Blatter, 257. N.W. Arabia, Mughaira, edge of Wadi Sirhan (K, January 1944); ibid., fixed sand dunes, about 750 ft. (H, 23. 12. 42).

Artemisia scoparia Waldst. & Kit.—Boiss., **3**, 364. Nejd, Khafs, near Riyadh (VF, 11840a, 23. 5. 43).

Artemisia herba-alba Asso—Blatter, 256. Nejd, silty bottom (VF, 13514, 1. 4. 44), forming a close stand; near Riyadh, silty bottom on stony plateau (VF, 11862a, 28.5.43).

Artemisia judaica L.—Blatter, 256. N.W. Arabia, Mughaira, southern edge of Wadi Sirhan (K, January 1944); Wadi Treef, 625 ft. (H, 28. 12. 42).

Senecio flavus (Decne.) Schultz Bip.—Blatter, 258. Nejd, Jebel Irkan, near Hail (K, February 1944); Jebel Salma (VF, 13544, 7. 4. 44).

Senecio desfontainei Druce. *S. coronopifolius* Desf. non Burm. f.—Blatter, 258. Nejd, Jebel Ajja, S.W. of Hail (K, 13. 3. 45); southern edge of Great Nefud, sandy hollows in gorges (VF, 1. 3. 43).

Calendula aegyptiaca Pers.—Schwartz, 291. Nejd, Jebel Salma (VF, 13544, 7. 4. 44); Jebel Irkan, Hail district, rocky ground (K, 15. 1. 45, VN Hinwa); Hail-Taima, granite sand (K, 8. 2. 44). N.W. Arabia, Qassani, sand dunes (H, 30. 12. 42, VN Sama'). Trucial Oman, Ras al Khaima, silty ground (VF, 13158, 29. 3. 44).

Osteospermum vaillantii (Decne.) Norlindh. *Tripteris vaillantii* Decne.—Schwartz, 291. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

Echinops glaberrimus DC. ex Decne.—Blatter, 262. Nejd, Aruma Plateau, wadi bed in stony plateau (VF, 11866g, 29. 5. 43).

Carduus pycnocephalus L.—Blatter, 264. Nejd, Jebel Salma, rocky gullies (VF, 13544, 7. 4. 44).

Centaurea eryngioides Lam.—Blatter, 267. Nejd, rocky mountains (VF, 13740A, 14. 5. 44).

Zoegea purpurea Fres.—Blatter, 266. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

Koelpinia linearis Pall.—Blatter, 271. Nejd, sand patches on gravel plain (VF, 13514, 1. 4. 44). S.E. Transjordan, Tubeik area, Luqa, mud flat (H, 29. 1. 43).

Picris babylonica Hand-Mazz. in *Ann. naturh.* (*Mus.*) *Hofmus. Wien*, **27**, 453, fig. 5 (2) (1913). Nejd, Hail-Taima, on hard granite sand soil (K, 8. 2. 44); Jebel Irkan, near Hail (K, February 1944); Wadi Rumma (VF, 13590, 13. 4. 44).

Picris damascena subsp. *blancheana* (Boiss.) Eig. *P. blancheana* Boiss., **3**, 741. Nejd, Jebel Salma (VF, 13544, 7. 4. 44).

Scorzonera tortuosissima Boiss., **3**, 775. Nejd, sandy ridges on stony plain (VF, 13528, 3. 4. 44).

Launaea mucronata (Forsk.) Muschl.—Schwartz, 295. Nejd, sand patches in gravel plain (VF, 13514, 1. 4. 44).

Reichardia tingitana (L.) Roth—Schwartz, 299. Nejd, Hail-Taima, granite sand (K, 8. 2. 44). N.E. Arabia, Manama, foothills (VF, 11620c, 12. 3. 43, VN Howa).

The genus Manilkara Adans.[1] in Brazil, seen by a field botanist.

By A. Ducke[2]

(Communicated by E. J. H. Corner, M.A., F.R.S., F.L.S. and N. Y. Sandwith, M.A., F.L.S.)

(Read 24 May 1957)

The American species of this economically important genus have been the object of several studies, but little advance has been made in their taxonomic knowledge in recent years. Like most trees of the American tropical rain forest, they are poorly represented in the herbaria, and the fruits, which in some species offer the best differential characters, are seldom available. Studies in the field, with extensive collections of flowering and fruiting samples from the same individual, are needed to improve the taxonomy of this genus, which cannot always be determined by flowering material alone.

With more than half a century of field work, I have had the opportunity of seeing many hundreds of these trees and of collecting complete botanical material from nearly all species known in the immense Amazon Valley. Some work has also been done in certain parts of the north-east Brazilian states, from Maranhão to Pernambuco. In 1950 I published a revision of the Amazonian species, with references to those of the other parts of Brazil ('As Massarandubas Amazônicas', *Anuário Brasileiro de Economia Florestal*, **3** (3), 231–244), soon followed by a review of the South American species by Joseph V. Monachino, 'The South American species of *Manilkara*', *Phytologia*, **4** (2), 94–118, 1952. Dr Monachino's review is based solely on flowering herbarium material, whereas in my case it has been possible to observe in the field and compare complete selected flowering and fruiting material; this difference gives rise to divergence in the concept of certain species, because fruits and seeds sometimes offer better differential characters than flowers.

It is my opinion, as well as that of several eminent taxonomists,[3] that names should be changed as little as possible; never in doubtful cases.

Manilkara is distributed throughout the world tropics and occupies a conspicuous place in the flora of Brazil, not so much because of the relatively small number of species but because of the value of its products: excellent timber for many purposes, good firewood, and various kinds of gum, most valuable of which are 'balata' (American gutta-percha) and 'chicle' (chewing gum); all fruits have sweet, edible pulp. The centre of distribution of the genus for the Americas is the Brazilian Amazon.

The vernacular name of most *Manilkara* species, in all Brazil, is 'massaranduba'; another name used for a few species is 'maparajuba' (*M. paraensis* and *siqueiraei*, in Pará) or 'maparajú' (*Manilkara longifolia* in Bahia and Espírito Santo). The widely distributed and, sometimes, very common *M. amazonica* is called 'massaranduba' in many localities (Óbidos, Belém, and State of Maranhão), but elsewhere (part of Pará and the basin of the Rio Negro) 'maparajuba'. *M. inundata* has been found in the Solimões basin designated as 'massaranduba'; on the Madeira and Purus as 'maparajuba'. *M. excelsa*, of the middle Tapajós, is known under both these names. The only Brazilian *Manilkara* without the above vernacular names is *M. bidentata* of the north-eastern boundary of Brazil, usually called 'balata verdadeira', because it yields a product of superior quality. Other species of *Manilkara* and other Sapotaceae which give an inferior product are sometimes called 'balata-rana' (false 'balata'). The name 'pendare', of Venezuelan origin, but widely used in the Territorio of Rio Branco (Brazil), apparently refers chiefly to chicle-yielding trees of the poorly studied *bidentata* complex.

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[1] Perhaps it would be better for *Manilkara* to continue as a section of *Mimusops* L.; this cannot be decided, however, without a study of the Old World species of both supposed genera. See Record and Hess, *Timbers of the New World*, p. 502 (1943), and Monachino, *Phytologia*, **4** (2), 95, 96, 1952.

[2] Supported by a grant from the Brazilian Consêlho Nacional de Pesquisas.

[3] 'We are maintaining the variety rather than treating it as a distinct species (at least until an extensive collection of flowering material has been made), primarily in order not to add to the nomenclature of the genus.' Krukoff and Monachino, 'The American Species of *Strychnos*', *Brittonia*, **4**, 293, 1942.

The identification of the species of *Manilkara* is not difficult in adult living trees, even in sterile condition, because each species has its own habit; it is difficult when dealing with herbarium specimens only. Most of the Brazilian species are deciduous trees, but are leafless only for a short time each year, usually at the beginning of the dry season (in northern and north-eastern Brazil) or that of the warm season (in southern Brazil). Their principal blossoming period coincides with the birth of the new foliage; such flowering twigs are often densely covered with blossoms having only very young leaves; some months later on the same tree, branchlets with adult leaves may bear a few flowers. The leaves of the heavily flowering branches usually remain smaller (often shorter) than those of the sparsely flowering ones; in this way, herbarium specimens from the same tree but collected at different seasons can easily be taken for different species. The only true evergreen Brazilian species I know is *M. triflora* of the coastal belt from eastern Pará to Rio Grande do Norte; it is common on dry 'tabuleiros' near Fortaleza where it is one of the few trees which never can be seen without full foliage.

The flowers of the Brazilian species of *Manilkara* do not exhibit the essential differential characters that are found in some exotic species; of most importance, relatively, is the staminode-shape which is quite variable within fixed limits for each species. The staminodes of *longifolia* and *bella* differ remarkably from those of all others because of their much broader, widely rounded form.

Fruits and seeds of *Manilkara* offer excellent characters for identification of certain species, but can hardly be found in the herbaria; for this reason, these characters have not been used by the authors whose studies are limited to herbaria. Specifically, as well as individually, their size varies within an established limit for each species. Their colour is remarkably constant in each species: the ripe fruits of *huberi*, *paraensis*, *excelsa*, *siqueiraei* and *inundata* are yellowish green, sometimes with some diluted purplish on one side; of *longiciliata*, *salzmannii*, *rufula*, *dardanoi* and *subsericea*, red (orange before maturity); of *amazonica* and *triflora*, black (orange-red when half ripe). The fruits of *longifolia*, of which I saw dried specimens collected by Kuhlmann, differ from all others by their larger size and more numerous seeds. The seeds have a fairly distinct dorsal keel in all species except *paraensis*.

The wood of *Manilkara* has been described by several authors, but no one has studied the differences existing among the Brazilian species of this genus. The late Prof. Record of Yale University received samples of *M. huberi* and *M. amazonica* from me, but no reference was made to the possible divergence in wood structure. It is well known, however, that the timber of 'massaranduba' is much more highly esteemed than 'maparajuba'. *M. huberi* has the most highly prized timber of the genus in Amazonia. It offers the advantages of yielding very large planks and of being abundant and easily accessible throughout its large geographical area (for example, along the Rio Guamá and the Bragança railway near Belém, along the lower courses of the rivers Paru, Trombetas, Tapajós and Madeira, and on the upland south of Parintins). *M. bella* of Rio and Espírito Santo is the best known non-Hylaean timber-yielding species.

The sixteen Brazilian species are distributed in the following manner:

Hylaea only: *siqueiraei*, *longiciliata*, *inundata*, *surinamensis*, *huberi*, *paraensis*, *excelsa*.
Hylaea and north-eastern South America: *bidentata*.
Hylaea and north-eastern Brazil: *amazonica*, *triflora*.
North-eastern Brazil: *salzmannii*, *rufula*, *dardanoi*.
South-eastern Brazil: *longifolia*, *bella*, *subsericea*.

In Pará State have been observed: *siqueiraei*, *huberi*, *paraensis*, *excelsa*, *amazonica*, *triflora* and *bidentata*; in the State of Amazonas: *longiciliata*, *inundata*, *surinamensis*, *huberi*, *amazonica* and *bidentata*.

New species are most likely to be expected in the rain-forest belt of southern Bahia and northern Espírito Santo, which is botanically much less explored than Amazonia.

SYNOPSIS OF THE BRAZILIAN SPECIES OF *MANILKARA*, MAINLY BASED ON OBSERVATIONS OF LIVING TREES

A. Leaves oblanceolate, very elongate, with main length of 180–250 mm., never more than 65 mm. broad, the young ones with very thin ferrugineous tomentum beneath. Staminodes broadly ovate, irregularly laciniate or denticulate. Fruit up to 40 mm. in diam., seeds up to 6. South of Bahia and north of Espírito Santo. *M. longifolia*

B. Leaves not excessively elongated, usually two to three times longer than broad. Fruits always smaller, seeds 1 or 2 per fruit.

  a. Leaves medium or large (up to 200 mm. long), beneath with dense sericeous tomentum having golden lustre, greyish when old. Staminodes broadly ovate, conspicuously multifid. States of Rio de Janeiro and Espírito Santo. *M. bella*

  b. Leaves with variously coloured tomentum or glabrous, not golden. Staminodes longer than broad.

    I. Leaves small or medium (mean length 30–90 mm.), with a thin layer of whitish or greyish subsericeous indumentum beneath, often becoming glabrous in age. Staminodes nearly as long as stamens with anthers, more or less bifid or trifid and often with a variable number of small lateral denticules. Fruit red. Restingas and hill forests of the coastal belt of the States of Rio de Janeiro and São Paulo. *M. subsericea*

    II. Leaves large or medium with very tenuous tomentum of microscopic hairs beneath, greyish with feeble silky lustre, the older ones often glabrate. Flowers medium sized, their tomentum greyish, not very persistent on the external sepals. Ripe fruits not seen; seeds (according to the Dutch authors) like those of *huberi*. Guianas, Venezuela (State of Bolivar) and the extreme north-east of Amazonian Brazil.
    M. bidentata (very probably a complex of more than one species)

    III. Young twigs, underside of young leaves, and peduncles and sepals, covered with thick, rusty to rufous tomentum, vegetative parts soon becoming more or less glabrate.

      1. Leaves 100–180 mm. long, thin (hardly subcoriaceous), nearly always with long acumen; tomentum homogeneous, of woolly, fasciculate hairs. Staminodes as long as the stamens with the anthers, simply bifid. Ripe fruits yellowish green, seeds with evident dorsal keel. Middle Tapajós.
      M. excelsa

      2. Leaves 24–90 mm. long, rigidly coriaceous, not acuminate.

        aa. Tomentum of the under-surface of the leaves double, of two kinds: woolly, soon detachable fascicles and simple, short hairs which persist after the former fall. Leaves obovate or elliptic. Staminodes shorter than the filaments of the stamens, merely bifid. Ripe fruits ovoid or subglobose, red. Subtropical mountain forests of north-eastern Brazil, from Ceará and southern Piauí to northern Bahia. *M. rufula*

        bb. Tomentum of the leaves uniform, woolly, in fasciculate bundles, soon falling and leaving the leaf glabrous. Leaves oblong-obovate. Staminodes as long as the stamens with the anthers, plurifid or irregularly bifid, or trifid and denticulate. Fruit oblong to fusiform, red. Tropical forest of Pernambuco. *M. dardanoi*

    IV. Leaves beneath with thin indumentum of yellow or yellowish hairs; very young and old leaves whitish or greyish. Sepals and peduncles with dense and persistent yellowish brown tomentum. Ripe fruits yellowish green, often on one side with a little purplish.

1. Leaves large or medium sized, the minute hairs of the under-surface conglutinated with resin; nerves glabrous, darker than the yellow background. Flowers large, peduncles 30 mm. or longer. Staminodes as long as the filaments of the stamens. Seeds compressed, with a distinct dorsal keel. Eastern and middle Hylaea. *M. huberi*

2. Leaves small, nerves of the under-surface inconspicuous. Flowers much smaller, peduncles not over 20 mm. long. Seeds smaller, turgid, without keel. Eastern Pará including the Amazon estuary, and north-western Maranhão. *M. paraensis*

V. Leaves glabrous, concolorous green on both sides when fresh (in dry samples often paler beneath).

1. Leaves ample, 50–200 mm. long. Flowers relatively large, peduncles relatively elongate (18–25 mm.).

aa. Staminodes as long as the stamens with the anthers, deeply and thinly bifid with very fine points. Ripe fruits red; seeds with distinct dorsal keel. Upland forests of Rio Solimões and Rio Negro. *M. longiciliata*

bb. Staminodes not longer than the filaments, shortly bilobate or with retuse apex. Ripe fruits yellowish green, seeds with less distinct keel. Swamp forests from the Pará estuary to north-western Maranhão. *M. siqueiraei*

2. Leaves small to medium sized (20–180 mm. long). Flowers small.

aa. Staminodes shorter than the filaments. Leaves of fertile branches more or less coriaceous. Flowers subglabrous, only the inner sepals tomentose. Fruits the smallest of the Brazilian species (diameter seldom more than 15 mm.), black when fully ripe; seeds with rather feeble dorsal keel.

aaa. Deciduous tree (at least in fertile age) of variable size. Flowers of full-blossomed twigs in rich fascicles, with the new foliage; staminodes shallowly bifid or bilobate, rarely shortly trifid. Fruit generally more or less globose. Most of Brazilian Amazonia; northern, western and central Maranhão. *M. amazonica*

bbb. Evergreen xerophilous tree of small size. Leaves not over 60 mm. long. Flowers 2–6 per fascicle, in axils of old leaves; staminodes often nearly entire. Fruit generally oblong, often on a very long and thin peduncle. Sandy littoral from eastern Pará to Rio Grande do Norte. *M. triflora*

bb. Staminodes half the length of the filaments, deeply bifid. Leaves elliptic-oblong, coriaceous when mature. Flowers subglabrous or with a thin tomentum on the external sepals. Fruit unknown. Upper Rio Negro, Cassiquiare, Rio Tonantins. *M. surinamensis*

cc. Staminodes as long as the filaments, rather shallowly bilobate (like *siqueiraei*). Leaves of fertile branches coriaceous. Flowers with conspicuous greyish tomentum. Ripe fruit red. Paraiba, Pernambuco, Bahia. *M. salzmannii*

dd. Staminodes as long as the stamens (with anthers), deeply and narrowly bifid. Leaves membranous or only slightly subcoriaceous, more often rather oblong. Flowers with distinct grey tomentum. Ripe fruits yellowish green, seeds distinctly keeled. State of Amazonas and Territories of Guaporé and Acre. *M. inundata*

ee. Staminodes about the same length as the complete stamens, more or less bifid with a variable number of small lateral denticules. Leaves small or hardly medium sized. Ripe fruits red. Restingas and hill forests of the coastal belt of Rio de Janeiro and São Paulo.
Forms with glabrous or glabrate leaves of *M. subsericea*.

(1) **Manilkara longifolia** (A. DC.) Dubard, *Ann. Mus. Colon. Marseille*, (3), 3, 22, 1915
Mimusops longifolia A. DC., *Prodr.* 8, 205, 1844.

Very characteristic, and isolated among the Brazilian species. Large tree of the rain-forest belt of southern Bahia and northern Espírito Santo, on humid sandy soil (according to J. G. Kuhlmann). I have seen only herbarium samples and young trees cultivated in the Jardim Botânico of Rio.

(2) **Manilkara bella** Monach., *Phytologia*, 4, 2, 104, 1952

Mimusops elata Fr. Allem, 'in litteris ad Martium' ex Miq. in Mart., *Fl. Bras.* 7, 42, 1863.
Mimusops elata Miq., in Mart., *Fl. Bras*, 7, 42, 1863, pro parte.
Mimusops elata Fr. Allem, in *Trab. Comm. Sci. Expl. Bot.* 3, 45, t. 2, 1866, pro parte (leaves in the description, and the fruiting twig in the drawing).
Mimusops elata Miq. sensu Ducke, *Arch. Jard. Bot. Rio*, 2, 13, 1918[1] and 3, 239, 1922.
Manilkara elata (Fr. Allem.) 'Chev.', Ducke, *An. Bras. Econ. Florestal*, 3, 3, 233, 1950.

According to Monachino, the type of *elata* is a plant of Martius's collection preserved in Munich which he considers conspecific with *huberi* Ducke of the Hylaea. Martius's plant, however, is sterile and comes from a region where *huberi* is unknown, and therefore Monachino's identification becomes doubtful. Monachino says (*loc. cit.* p. 101): 'Erroneous locality given in the original description: *silvas prov. Sebastianopolitanae*[2] *et Bahiensis: Mart.* Data on photo of Martius' plant at Herb. Regium Monacense: *silvas prov. Bahiensis etc. e.g. ad Ferradas, Martius* 1819? In 1819 Martius traveled in both Pará and Bahia (*Fl. Bras.* 1, 60).' In Monachino's opinion, *elata* F. Allem. ex Miq. is conspecific with *huberi*, and the locality on its label *must* therefore be erroneous, but it is also possible that the locality was right and the identification erroneous! Martius's sterile specimen may belong to still another species, perhaps undescribed; nobody can prove otherwise because sterile samples of *Manilkara* are not always identifiable, even when not 130 years old. We surely shall not replace the widely accepted name of a completely known plant (*huberi*) by another of very doubtful identity.

A well-preserved floriferous specimen of Allemão's type collection of *elata* Fr. All. is at the Jardim Botânico of Rio; the locality on its label is Rio; it is the same species as Glaziou 12071 from Petropolis, type of *bella*. Very likely Miquel saw Allemão's collection, because Allemão would send duplicates of his new Rio plants to Martius and collaborators. Allemão, later, confused his *elata* from Rio with the north-east Brazilian *rufula* Miq., to which belong his Ceará specimens labelled *elata*, preserved in the Museu Nacional. Monachino refers to this confusion in the following manner (p. 101): 'Ducke, apparently giving weight to locality cited and credit given to Allemão in Flora Brasiliensis, judged the Allemão collection from Ceará (*M. bella* Monachino) typified *elata*. He identified the Pará material as *M. huberi*, a view that has been followed by Eyma and others.' There is, however, a mistake: I never judged that Allemão's *elata* from Ceará was Allemão's *elata* from Rio, cited in *Flora Brasiliensis*! On p. 103, Monachino himself says: 'Ducke informs me that a collection by F. Allemão from Ceará, labelled *M. elata*, is this plant' (*M. duckei* Mon. = *rufula* Miq.). '*M. elata* of Allemão (1866, p. 45) is in part this plant (Ducke, 1918, p. 15).' Thus, the same author states that my identification of *elata* was not based on Allemão's plant from Ceará but on Allemão's earlier collection from Rio. Huber identified the Pará 'massaranduba' with the southern *elata* before having seen flowers of the Pará plant; later he planned to describe it as new but died before it was done. Allemão states that 'massaranduba' occurs in Brazil from Pará to Santa Catarina; he evidently was ignorant that this vernacular name belongs to several species.

From the above evidence it seems that *elata* Fr. All. ex Miq. should be rejected as a *nomen confusum, mixtum compositum* of two species, one (*bella* Mon.) definitely identified, the other dubious. It is impossible to ascertain the true 'type', because, in 1863, this concept in the modern sense had not yet been invented.[3]

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[1] The analysis of the flower is confused with *M. rufula*.

[2] Locality of the plant collected by Freire Allemão and cited in the description by Miquel. The plant from Bahia is the other, collected by Martius.

[3] At that time botanists used to describe a complex *species* indicating the supposed limits of its variability; these descriptions were often based on several to many botanical samples. Now authors more often describe a specimen and not the species. The type concept really does avoid many mistakes, but, on the other hand, deprives systematics of a great deal of its scientific value: too many recent binomials are names of herbarium sheets and nothing more.

M. bella seems to be restricted to the rain forests of south-eastern Brazil (Rio de Janeiro and Espírito Santo). To-day it is a rather rare tree, at least where those States are more densely settled. Floriferous specimens from the State of Rio are in the Museu Nacional (collection Saldanha da Gama, without exact locality, and Glaziou 12071, from Petropolis, type collection of *bella* Mon.) and in the Jardim Botânico (type collection of *elata* Fr. Allem. *in litt. ad Martium*). Floriferous material was collected by Kuhlmann (no. 417) in Espírito Santo (Rio Doce, Linhares). I myself observed only one living plant, a young tree in the forest of the Serra de Friburgo, State of Rio. This species is not found in the Federal District of Brazil; it may once have existed there but has long since been eliminated because of its excellent timber (the best 'massaranduba' of the region). Allemão's type collection is labelled 'Rio de Janeiro' without indication of the exact locality (city or state).

(3) **Manilkara huberi** (Ducke) Chev., *Rev. Bot. Appl. Agr. Trop.* **12**, 276, 351, 1932

Mimusops huberi Ducke, *Arch. Jard. Bot. Rio*, **2**, 14, 1918.
Mimusops elata Miq., in Mart., *Fl. Bras.* **7**, 42, 1863, pro parte.
Mimusops elata Fr. Allem. sensu Huber, *Bol. Mus. Goeldi*, **4**, 436, 1904.
Manilkara elata (Miq.) Monach., *Phytol.* **4**, 2, 101, 1952.

As just stated, *huberi* is, according to Monachino, a synonym of *elata* Fr. All. ex Miq. and its name must therefore be replaced by the latter. But *elata* Fr. All. ex Miq. is a 'mixtum compositum' of *bella* Mon. (=*elata* Fr. All. *in litt. ad Martium*) from Rio, and of a species from Bahia which Monachino identified, through a single leaf of the sterile sheet he had seen, as equal to the Hylaean *huberi*, in spite of coming from a region where the latter has never been observed. Monachino was convinced that the leaf he had seen was the type[1] of Miquel's description and that it belonged to the above-cited Hylaea species; he states that the locality given in the original description and on the label of Martius's plant *must* be erroneous (p. 101). But perhaps the locality was correct and the identification erroneous; a single leaf or even a sterile sheet is not sufficient for the exact identification of a *Manilkara*. Monachino says: 'I choose to believe that actually the type of *M. elata* was collected in northern Brazil, rather than assume that a species with leaves like it remains un-rediscovered in southern Brazil' (p. 102); in my opinion, however, the rain-forest belt of Bahia is the part of Brazil most likely for a new species of forest trees. And, as to the exactness of the identification of Martius's plant, see Monachino, *loc. cit.* (p. 102), quoting a letter from Prof. Suessenguth of Munich: 'We have compared the fragment of *M. huberi* sent by you with our type of *M. elata*. An exact identification, naturally, is not possible with respect to the small material.' From all this it becomes very evident that nothing is to be gained by replacing an established name of a well-studied species by another, riddled with doubt!

This species is sometimes confused with 'fine balata' yielding trees belonging to the poorly studied *bidentata* complex. Monachino writes (p. 101): 'A. J. Sampaio told Chevalier verbally that *M. huberi* is a good producer of "balata" and that in the Óbidos–Tumuc-Humac region (expedition Rondon) it is the most frequent and tallest tree, as abundant in the forest area of the river as on the chain of Tumuc-Humac Mts.' However, the trees seen along the river were most certainly *huberi*, while those on the mountains were probably *bidentata*. The former yields a very inferior quality of 'balata', exported under the name 'massaranduba'; it is chiefly used for its excellent timber.

M. huberi attains the greatest average size (30–40 m.) of all Amazonian species, and the largest trees may exceed 50 m. The live plant is easily recognizable by the colour and the indumentum of the leaves. The fruits are more or less globose, about 30 mm. in diameter, yellowish green and somewhat pinkish on one side when fully ripe; the seeds, which resemble those of a small 'sapotilla', are laterally compressed, with well-developed longitudinal dorsal keel.

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[1] See the preceding footnote.

M. huberi is widely distributed in the eastern half of the Hylaea, from Dutch Guiana to the north-west of the State of Maranhão (upper Pindaré basin, Fróes) and from the Atlantic belt to the middle Rio Negro and the Territories of Rio Branco (Serra Grande, Caracaraí) and Guaporé (common around Porto Velho and Salto Teotonio). It is very frequent near Belém; it has not yet been observed in the drier forest of the immediate vicinity of the lower Amazon river nor around Manáus. It occurs in the virgin rain forest of the 'terra firme' as well as some less flooded 'várzea' land.

The wood of *M. huberi* is the most esteemed of all 'massarandubas' of Brazilian Amazonia, but the latex yields a very low-class 'balata', exported under the same name as that of the tree ('massaranduba'). The fruits, which are edible like those of all other species, are sometimes sold on the market of Belém.

(4) **Manilkara paraensis** (Huber) Standl., *Trop. Woods*, **34**, 41, 1933

Mimusops paraensis Huber including var. *discolor* and var. *densiflora* Huber, *Bol. Mus. Goeldi*, **4**, 435, 1904.

Mimusops maparajuba Huber, loc. cit., seeds only.

A medium or fairly tall tree reaching only exceptionally 30 m.; leaves resembling minor leaves of *amazonica* but with the lower surface more or less yellowish, due to a layer of microscopic hairs with some resin (not always easy to see in herbarium specimens); flowers as in *amazonica* but densely tomentose and with long staminodes, their peduncles usually strongly recurved; fruits a little larger than those of *amazonica*, ellipsoid or subglobose, pale yellowish green, somewhat pink on one side when fully ripe; seeds small for the genus but larger than in *amazonica*, distinctive on account of their turgid dorsal side without the longitudinal keel more or less conspicuous in all others.

M. paraensis grows in humid or slightly swampy virgin rain forest of 'terra firme', but never in true 'igapó' nor in the periodically flooded 'várzea'. It has been observed in the eastern part of the State of Pará (Amazon estuary up to Gurupá; near Belém and along the Bragança railway; Rio Capim) and north-western Maranhão (upper Pindaré, col. Fróes).

(5) **Manilkara bidentata** (A.DC.) Chev., *Rev. Bot. Appl. Agr. Trop.* **12**, 270, 1932

Mimusops bidentata A. DC., *Prodr.* **8**, 204, 1844. Synonymy referring to specimens from the Antilles, Venezuela and the Guianas, referred to this complex, cf. Cronquist, *Bull. Torrey Bot. Cl.* **72** (6), 553, 1945.

In accordance with most authors *M. bidentata* is the name of a complex possibly including several species (old and new) and first used for the 'fine balata' of the Guianas. Field work in widely separated stations of the large area to which this complex belongs is much needed to decide this question. The first step in breaking down this complex should be the grouping of the trees on the basis of their latex types; viz. 'balata' (sticky) or 'chicle' (not sticky). This must be done by woodsmen experienced in the extraction of these products, followed up by the collection of complete botanical material from trees chosen in each group, and the fruits should not be ignored for the simple reason that they are rarely available in herbaria! Finally must come the comparison of these collections with the herbarium types corresponding to the many names used in this complex. The isolated study of these venerable though usually incomplete and often badly preserved relics cannot solve this problem. The economic importance of the trees of this complex has given rise to an extensive literature chiefly aimed at interpreting older names.

I have seen only a few incomplete specimens attributed to *bidentata*, most of which possessed a tenuous greyish indumentum on the lower surface of the leaves; others had glabrous leaves. The latter resemble either *amazonica* or *siqueiraei*; both these species occur in the well-explored region around Belém where no 'fine balata' yielding trees are known (*M. huberi*, also common here, yields a low-grade balata, known as 'massaranduba'). The Venezuelan name 'pendare', much used in the Brazilian Territory of Rio Branco, is applied to 'chicle' and not to 'balata', according to reliable information (Fróes *et al.*). However, Monachino (loc. cit., p. 113) identifies a plant labelled 'pendare', from Venezuela, as *bidentata*, and I myself attributed a 'pendare' from Rio Branco to the same species; it is impossible to ascertain the origin of any error that may have been made. According to Fróes, the name 'pendare' is often also applied to 'chicle'-yielding Apocynaceae. The 'jaune d'œuf' of French Guiana, attributed by Chevalier to *M. bidentata* (see Monachino, loc. cit., p. 112), is not a 'balata' at all but *Pouteria rivicoa* ('cutitiribá' of Pará), native to the Hylaea and often cultivated for its edible fruits. The use of the latex is unknown.

First-class 'balata' is obtained only from trees growing on the high plateau in the interior of the three Guianas and adjacent highlands of Brazil and Venezuela, collectively known in botany under the name *M. bidentata*. The type of this must correspond to one of the species making up this complex. In Brazil, these trees have been found in the extreme north of Pará (Tumuc-Humac chain), the northern half of the Territory of Rio Branco, and the extreme north-east of the State of Amazonas (mountainous country east of the upper Rio Negro). The West Indian species attributed by Cronquist to *bidentata* must certainly be different; I examined three flowers from a specimen from Tortola, Virgin Islands (Beard 318, cited in the Cronquist monograph), and found staminodes as long as the filaments, entire with a sharp point as well as some small lateral teeth. Were this West Indian species a true 'balata', it would surely be explored industrially.

The plants with glabrous leaves which most authors consider a form of *M. bidentata* resemble the Pará 'maparajuba', *M. siqueiraei*, as pointed out by Monachino. I am unable to decide whether the latter corresponds with one of the several names now considered synonyms of *bidentata* by many authors; I am, however, sure that it is a well-defined species and that its latex does not yield 'balata'.[1] The name 'maparajuba' is never used for 'balata'.

Ule 8728, from Rio Cuquenán, vicinity of Roraima, has been identified (in Dahlem) as *bidentata*, but its label has the vernacular name 'massaranduba', never applied to good 'balata' trees. Its leaves are very hard and entirely glabrous; the flowers of the specimen I saw were not yet adult; they were covered with a layer of glutinous resin. A plant from British Guiana, which Monachino refers to a 'strongly resiniferous form or variety of *M. bidentata*, with rigid glabrous leaves', might be conspecific with Ule's plant; it is called 'black balata' and 'said to have plentiful latex which does not coagulate' (Monachino, loc. cit., p. 113).

(6) **Manilkara amazonica** (Huber) Chev., *Rev. Bot. Appl. Agr. Trop.* **12**, 276, 1932

Mimusops amazonica Huber, *Bol. Mus. Goeldi*, **4**, 433, 1904.
Mimusops maparajuba Huber, *Bol. Mus. Goeldi*, **4**, 434, 1904, excl. seeds.
Mimusops reticulata Huber ex Ducke, *Bol. Mus. Goeldi*, **7**, 174, 1913, nomen nudum.
Manilkara surinamensis (Miq.) Dubard, *sensu* Monach., *Phytol.* **4**, 2, 111, 1952, pro parte.

In Monachino's opinion this species does not differ from *surinamensis*, and is therefore cited by him as a mere synonym. This may be so but can only be confirmed by complete material of the true *surinamensis*, and most important are the fruits which are still unknown. The widespread, common (in many places) and well-studied *amazonica* is variable in the leaf form and the staminode type, but of the hundreds of fruits I have seen (and often eaten) all were invariably very small (for the genus), black when fully ripe (red when half ripe), and with small seeds with a feeble dorsal keel. The staminodes of *amazonica* are variable as in most species of *Manilkara*, but I have never seen them so deeply and regularly bifid as in *surinamensis*; the presence of three quite different forms of staminodes in the same flower of *amazonica* (in Ducke 189) is abnormal. In *amazonica* the leaves are longer, thinner and less reticulated in rain-forest trees; shorter, thicker, harder and with very conspicuous prominent reticulation in the low, often shrubby individuals growing in 'campinas' (open spots on white sand) and on shores of lakes with clear or black water. *M. reticulata* Huber, nomen nudum, cited by Monachino, is a herbarium specimen of the latter; it was collected on a campina east of the Mapuera, tributary of the Trombetas. In the State of Maranhão and the eastern littoral of Pará a form of *amazonica* with relatively short, broad, obovate leaves occurs. There could be no advantage in naming this form which is connected by every degree of transition from the common narrow-leaved form; both are very common near S. Luiz, Maranhão, where they grow together.

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[1] According to research done by R. L. Fróes (formerly botanist of the Chicle Development Company), the latex of *siqueiraei* is very like that of *amazonica*; it is sticky when fresh and can furnish a good chewing gum but no 'balata'.

The type of *amazonica* labelled 'massaranduba', Herb. Mus. Pará 2527, came from Castanhal on the Bragança railway; it was not collected by Huber nor any known botanical collector but apparently is a twig picked by a casual passer-by from a low mature branch with a few dense relatively large leaves and a few flowers past anthesis. In the 'Museu Goeldi' park there are four trees introduced by Huber as *amazonica*, but only one tree belongs to this species, the others are *M. siqueiraei*. The type of *M. maparajuba*, Herb. Mus. Pará 855, called 'maparajuba', belongs to the form of *amazonica* which has smaller and firmer leaves showing a tendency to inroll, frequent on sandy beaches and 'campinas'; the flowers of the type collection are past flowering and there are no fruits. The seeds described by Huber ('semen turgidum dorso rotundatum') and attributed to both *maparajuba* (=*amazonica*) and *paraensis*, all belong to *paraensis*. The types of both were collected from the same place with the same vernacular name and registered in the herbarium with the same number 855, only later subdivided in 855 (*maparajuba*) and 855*a* (*paraensis*).

M. amazonica, in rain forest, is a rather large tree often over 20 m. high; in summer-dry woods, a small to medium tree; in the open spots of white sand with black humus, called 'campinas', a treelet or a shrub sometimes less than 2 m. high. It usually grows on sandy soil, on upland as well as on slightly inundable or marshy ground, in Amazonia often along rivers and streamlets with limpid or 'black' water, never in 'várzea' flooded by 'white' (muddy) water. It blossoms abundantly in multiflorous fascicles after the fall of the foliage, at the beginning of the dry season; later may appear a few flowers in the axils of mature leaves.

In many places *M. amazonica* is the most frequent species of the genus. Its area, according to the collections available, includes: the State of Pará (with the probable exception of the middle Tocantins and the Araguáia); the eastern half of the State of Amazonas, the Solimões up to Igarapé Belém near the Colombian border and the Rio Negro basin from Manáus to the Uaupés and Issana rivers; the territories of Rio Branco (Caracaraí) and Amapá (Oyapoc); a large area of the State of Maranhão, not only in the Hylaean north-west (upper Pindaré, coll. Fróes), but also very frequent near São Luiz and up the Rio Itapecuru to Codó. No specimens have been seen from the Territories of Guaporé and Acre, nor have any references been made by authors to presence in the Guianas and in the neighbouring republics.

M. amazonica was second only to 'sorva grande' (*Couma macrocarpa* Barb. Rodr., fam. Apocynaceae) in furnishing 'chicle' in the lower Rio Negro basin.

(7) **Manilkara triflora** (Fr. Allem.) Ducke, *An. Bras. Econ. Florestal*, **3**, 3, 238, 1950

Mimusops triflora Fr. Allem., *Trab. Comm. Sci. Expl. Bot.* **1**, 50, t. 13, 1866.
Mimusops glaziovii Raunkiaer ex Warming, *Vidensk. Meddel. Nat. Foren.* p. 863, 1889, pro parte.
Mimusops cearensis Huber, *Bull. Herb. Boiss.* (2), **1**, 320, 1901.

Low tree or shrub of the coastal belt from eastern Pará (Salinas) to Rio Grande do Norte (Natal), on old dunes or high beaches often along mangrove, common around Fortaleza (Ceará) on the sandy 'tabuleiros' of remote maritime origin where some trees may reach up to 8 m. in height (the largest examples have a long time ago been destroyed). So closely allied with *M. amazonica* that I sometimes thought it would be a depauperate form of this species, but *triflora* is an evergreen typically xerophilous tree, *amazonica* a deciduous tree which sheds the foliage each year at the beginning of the dry season. A plant of *triflora* cultivated in the Pará Museum from a seed from Parnaiba (Piauí) preserved all the morphological characters of the native trees of the sea coast.

(8) **Manilkara salzmannii** (A.DC.) Lam, *Blumea*, **4**, 356, 1941

Mimusops salzmannii including var. *mucronata* A.DC., *Prodr.* **8**, 205, 1844.
Mimusops glaziovii Raunkiaer ex Warming, *Vidensk. Meddel. Nat. Foren.* p. 863, 1889, pro parte.

Very close to *M. amazonica*, from which it differs only by having more tomentum on the peduncles and sepals, longer staminodes, and larger orange red to bright scarlet fruits when ripe. I have not seen type material but I have seen a Pickel specimen from Pernambuco, identified in Germany. This is the common 'massaranduba' of the sandy 'restingas' and 'tabuleiros' around Recife where it occurs in the form of low trees with relatively large leaves; in the hill forests (Dois Irmãos, for example) it is rather tall (up to 20 m.), with smaller (chiefly narrower) leaves. The geographic area of the species comprises the coastal belt from Paraiba down to the State of Bahia.

(9) **Manilkara siqueiraei** Ducke, *Trop. Woods*, **71**, 24, 1942

A rather tall tree; leaves and flowers of the same size as those of *longiciliata* and *huberi*, which are among the largest of the Brazilian species; leaves on both surfaces green when fresh, glabrous and shining. Flowers with peduncles and external sepals nearly glabrous (like *amazonica*), the staminodes equal or slightly shorter than the filaments and only shallowly bilobate at the apex (nearly retuse); fruits resembling those of *huberi* and *longiciliata* in form and size but colour like those of *huberi*; seeds less compressed than in *huberi* and *longiciliata* and consequently with a less developed dorsal keel. Sterile samples can be confused only with *longiciliata*.

M. siqueiraei is not rare on the Pará estuary islands and along the Rio Pará, where it is always found in swamp forest along secondary streams or channels flooded by the water rising with the Atlantic tides. I collected flowering material in the mangroves of the Rio Magoari north-east of Belém (Ducke 975, type) and the Rio Aramá of the Pará estuary (Ducke, Herb. Jard. Bot. Rio 22197). Fruits were obtained from the type tree. Floriferous specimens collected in the Hylaea of north-western Maranhão (upper Pindaré, Fróes 20344) resemble the above-cited specimens. Huber never saw botanical material of this species; however, he left three cultivated specimens of the species in the garden of the Pará Museum, along with one specimen of *M. amazonica*, all of which he labelled *M. amazonica*. The diversity of these plants was discovered by my old friend and colleague in work at the Pará Museum, Rodolpho Siqueira, who called my attention to it.

M. siqueiraei resembles what most authors include in their concept of *bidentata*. *M. bidentata*, however, is nothing more than a complex of forms possibly including more than one species. *M. siqueiraei* does not yield 'balata'[1] and therefore cannot be placed in the complex known as 'fine balata'; however, it can belong to the herbarium complex of *M. bidentata* and its supposed synonyms.

(10) **Manilkara surinamensis** (Miq.) Dubard, *Ann. Mus. Col. Marseille*, (3), **3**, 22, 1915; Monach., *Phytol.* **4**, 2, 111, 1952, pro parte

Mimusops surinamensis Miq., in Martius, *Fl. Bras.* **7**, 43, 1863.

According to Monachino, *M. amazonica* should be conspecific with this plant but our specimens differ in the somewhat larger leaves, more abundant indumentum, and the narrowly bifid staminodes. He forgets, however, that the fruits of true *surinamensis* are as yet unknown, and that fruits and seeds yield some of the best differential characters for *amazonica*. We must therefore refrain from uniting the two species until we can obtain fruits of typical *M. surinamensis*.

In contrast to the common *M. amazonica*, which occupies the largest known area of the Brazilian *Manilkara* species, *surinamensis* has been observed only in the basin of the upper Rio Negro and Cassiquiare reaching into Brazil, Venezuela and Colombia, and on the Rio Tonantins, a small tributary of the Solimões, situated between the large Içá and Japurá rivers. The medium-size trees inhabit 'igapó' and low, often deeply flooded 'restingas' along the shores of these rivers, where scanty material, with flowers alone (for the most part old), was collected by Baldwin, Ducke, Fróes and Spruce. All specimens of the Baldwin and Fróes collections came from trees felled for 'chicle'. Some of the recently collected specimens are identical with Spruce 3351, of which I saw a duplicate at the herbarium of the Jardim Botânico, Rio. This plant was described by Miquel; the other, from Surinam, cited by the same author, is a very incomplete specimen of the *bidentata* complex, according to Eyma. Thus, *M. surinamensis* is unknown in Surinam!

(11) **Manilkara longiciliata** Ducke, *Trop. Woods*, **71**, 22, 1942

Leaves and flowers in size and indumentum like *siqueiraei* but the staminodes like *inundata*; fruit like *huberi* and *siqueiraei* in size and shape but bright orange-red when fully ripe; seeds like *huberi*. A medium-sized or large tree of the upland rain forest along the Solimões (Esperança, at the mouth of the Javarí, type locality; collected by 'chicle' explorers from Manaquirí and Paraná dos Mundurucus and received through Mr N. A. Adams and Dr Sócrates Bomfim); collected by Fróes on Rio Padauirí, basin of the lower Rio Negro. It yields a good 'chicle' but is not frequent enough to be economically important.

(12) **Manilkara inundata** (Ducke) Ducke, *Trop. Woods*, **71**, 22, 1942

Mimusops inundata Ducke, *Arch. Inst. Biol. Veg. Rio*, **4**, 58, 1938.

Large tree (30 m. or more); leaves thinner (hardly subcoriaceous) and more oblong than in the other Amazonian species; flowers in most characters like *amazonica* but the sepals evidently tomentose and the staminodes with length and shape of *longiciliata*; only fruits with rather decayed pericarps were seen, they were apparently like *huberi*; seeds like *huberi* and *longiciliata*. Growing in rain forest on swampy ground of 'terra firme' and in 'várzea' along rivers of the State of Amazonas and the Territories of Guaporé and Acre: lower Rio Madeira, shore opposite to Humaitá (type locality) and near Tres Casas (Krukoff); Rio Ouro Preto, basin of the Mamoré (coll. Kuhlmann); Rio Juruá: Fóz do Embira and Bôca do Macauan (Krukoff 4745 and 5496, distributed as

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[1] See footnote, p. 651.

M. excelsa), and Esperança at the mouth of the Javarí (Ducke). Sterile trees have been seen in 'várzea' forest along the upper Solimões and the Middle Purus. Nowhere does this species furnish 'chicle' or 'balata'.

(13) **Manilkara excelsa** (Ducke) Standl., *Trop. Woods*, **34**, 41, 1933

Mimusops excelsa Ducke, *Arch. Jard. Bot. Rio*, **3**, 235, 1922.

A tree which can reach the huge proportions of *M. huberi*; however, small flowering trees are sometimes found in rocky sites. Easy to recognize by its leaves which are generally complicate-acuminate (young ones covered with rusty tomentum like the innovations) and by its flowers with a conspicuous rufous tomentum. Ripe fruits nearly globose, the size and colour of a common olive; seeds moderately compressed, with an evident dorsal keel.

This species seems to be restricted to the periodically flooded forests along the rapids of the Tapajós, from the foot of the lowest of these to the border of the States of Pará, Amazonas and Mato Grosso.

(14) **Manilkara rufula** (Miq.) Lam, *Blumea*, **4**, 356, 1941

Mimusops rufula Miq., in Mart., *Fl. Bras.* **7**, 44, 1863.
Mimusops rufula Miq. sensu Ducke, *Arch. Jard. Bot. Rio*, **2**, 15, 1918[1] and **3**, 239, 1922.[2]
Mimusops elata Fr. Allem., *Trab. Com. Sci. Expl. Bot.* **3**, 45, t. 2, 1866, pro parte (with exclusion of the leaves in the description, and of the fruiting twig in the drawing).
Manilkara duckei Monach., *Phytol.* **4**, 2, 103, 1952.

The type of *rufula*, Gardner 2910 from Piauí, and the paratype from Pernambuco, are probably from the same tree. They are certainly from the same mountainous region on the border line of those former provinces which in Gardner's time were vaguely delimited. I saw two photos of the Gardner collection, very poor specimens with old flowers lacking corollas and with a young fruit, thanks to the kindness of Dr Monachino; the type of *M. duckei* Mon. (Dárdano de A .Lima 49–168), on the contrary, is an exuberant flowering specimen from the subtropical rain forest of Serra Negra (1000 m.), Pernambuco. Both represent extreme forms of herbarium specimens of this species, which is highly variable in the length of its petioles as well as in the form of the blades, which can be obovate or (less commonly) oblong-elliptic; the indumentum varies chiefly in durability, often being reduced in old leaves to a thin layer of greyish simple hairs which persist after the rufous, fasciculated, woolly hairs (Monachino saw these hairs on the leaves of the paratype of *rufula*; cf. loc. cit., p. 108, under *M. dardanoi*). The veins of very old leaves often become quite inconspicuous. Several specimens, of the many I have seen, are a good match for the photos of the type collection of *rufula*, including the young fruit, and differing only in having longer petioles. Two flowering specimens from Ceará, Serra de Baturité, Ducke Mus. Pará 1428 and 2028, cited by Monachino as *M. duckei*, have been identified by Charles Gilly (1942) as *rufula*.

Allemão, loc. cit., confused *rufula* with his *elata* from Rio (=*bella* Mon.), but his later collection from Ceará (Serra d'Aratanha, Pacatuba, labelled *elata* and preserved in the Museu Nacional of Rio) really is *rufula*. I cannot understand why Monachino (loc. cit., p. 108) writes '*M. rufula* in the sense of Ducke is *M. bella*'!

This is the only 'massaranduba' known from the subtropical forests of the plateaux and mountains of north-eastern Brazil: Ceará (Serras of Maranguape, Baturité and Aratanha); south-eastern limit of Piauí; Paraiba (Areia); Pernambuco (Serra Negra and Garanhuns, often common here; Bahia (Ibiquara). It grows in altitudes from 700 to

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[1] Except for the analysis of the flowers in which the floral drawing was confused with *bella* Monach. (=*elata* Fr. Allem. *in litt. ad Martium*).

[2] The analysis of the flower (p. 239) is confused with that of *M. huberi*.

1000 m., with an annual mean temperature of 20 to 21° C. It is most unlikely that such a common tree would have escaped the attention of Gardner, or that Gardner's plant would not have been rediscovered by some of the rather numerous botanical collectors who have worked in the region since Gardner's time; this strengthens my opinion that *duckei* Mon. is conspecific with *rufula.*

M. rufula is one of the three Brazilian species with thick rufous tomentum on the young parts. It differs from the others by the double tomentum on the leaves; it differs from *dardanoi* not only by this character but also by the ellipsoid or subglobose fruits; from *excelsa* by its thick, coriaceous, more or less obtuse leaves and red fruits. The trees are medium to large sized.

(15) **Manilkara dardanoi** Ducke, *An. Bras. Econ. Florestal*, **3**, 3, 243, 1950

The type-tree was discovered in flower in July 1950, by the agronomist Dárdano de A. Lima, botanist of the Instituto de Pesquisas Agronômicas of the State of Pernambuco; it was destroyed before fruiting. In 1951 the same botanist and I found several trees with flowers and later with ripe fruits. All grow in a restricted area along the Aldeia road near Recife, at the beginning of a low plateau behind the city; the rather sandy soil here is covered with shrubs and low trees, apparently an old secondary formation. No trees exceed 6 m. here, but taller trees may occur in the remnants of primary forest. The same happens with *M. salzmannii*, the common 'massaranduba' of Recife, which may reach 20 m. in the forest at least partially primary on the hills of Dois Irmãos, but in the maritime 'restingas' it is always a low tree.

M. dardanoi differs from *rufula* by the readily and fully detachable homogeneous tomentum of fasciculate hairs, by staminodes not unlike those of the southern *subsericea*, and by the oblong to nearly fusiform fruits with much longer and narrower seeds. It is a rare tree of the tropical forest belt ('zona da mata') accompanying the coast of Pernambuco, while *rufula* is a common characteristic tree of the subtropical plateau and mountain forests.

(16) **Manilkara subsericea** (Mart.) Dubard, *Ann. Mus. Colon. Marseille*, (3), **3**, 22, 1915

Mimusops subsericea Mart., *Flora*, **22**, Beibl. 1, 3, 1839.
Mimusops subsericea var. *acmanthera* Miq., in Mart., *Fl. Bras.* **7**, 43 bis, 1863.
Mimusops floribunda Mart., *Flora*, **22**, Beibl. 1, 3, 1839.
Synarrhena floribunda (Mart.) Fisch. et Mey., *Bull. Sci. Acad. Petrop.* **8**, 256, 1841.

A polymorphic species or perhaps a complex of more than one species; still insufficiently studied in spite of the frequency of some forms in the hill forest and the maritime 'restingas' around Rio de Janeiro. Indumentum and staminodes are extremely variable; fruits and seeds of the various forms need further study. The fruits of the small trees occurring in the 'restingas' of Rio are subglobose to oblong, seldom over 25 mm. long, red when fully ripe. *M. floribunda*, described from the 'restinga' of Cabo Frio, State of Rio, seems to be the glabrous form of the present species, not rare in the 'restingas' of Rio, along with the more common typical form. A specimen from that locality (Netto, Glaziou and Schwacke, September 1881, Museu Nacional 93971) has perfectly glabrous adult leaves, but the under-surface of the youngest leaves has the pubescence characteristic of *subsericea* and undoubtedly belongs to this species. A specimen from the littoral of São Paulo (Santos) has remarkably large, glabrous leaves.

The diatom community of some Bryophyta growing on sandstone.

By F. E. Round, Department of Botany, University of Bristol.

(With 28 Text-figures)

(Communicated by Dr J. W. G. Lund, F.L.S.)

[Read 24 May 1957]

Samples of Bryophyta from a small sandstone cliff in Brotherton Park, Cheshire, have been investigated in order to determine the composition of their attached diatom communities. As far as the author is aware no similar community has been studied in this country. The cliff is in a tree-shaded region of the park, and at the time of collecting was quite moist due to water seeping down from soil on top of the cliff, whilst at other times it may be dry.

Sample I. *Lophocolea bidentata* (L.) Dum. from a very wet region of the rocks.

Sample II. *Cephalozia bicuspidata* (L.) Dum. and some *Calypogeia trichomanes* (L.) Corda growing in dense mats.

Sample III. *Eurhynchium praelongum* Hobkirk at the base of the wet cliff.

Sample IV. *Pellia epiphylla* (L.) Corda, on the rock face.

Sample V. A mixture of *Cephalozia bicuspidata* (L.) Dum. and *Pellia epiphylla* (L.) Corda on the vertical wet rock face.

Sample VI. *Cephalozia bicuspidata* (L.) Dum. on the wet rock.

Care was taken during sampling to avoid as far as possible contamination with soil since this also harbours a characteristic flora.

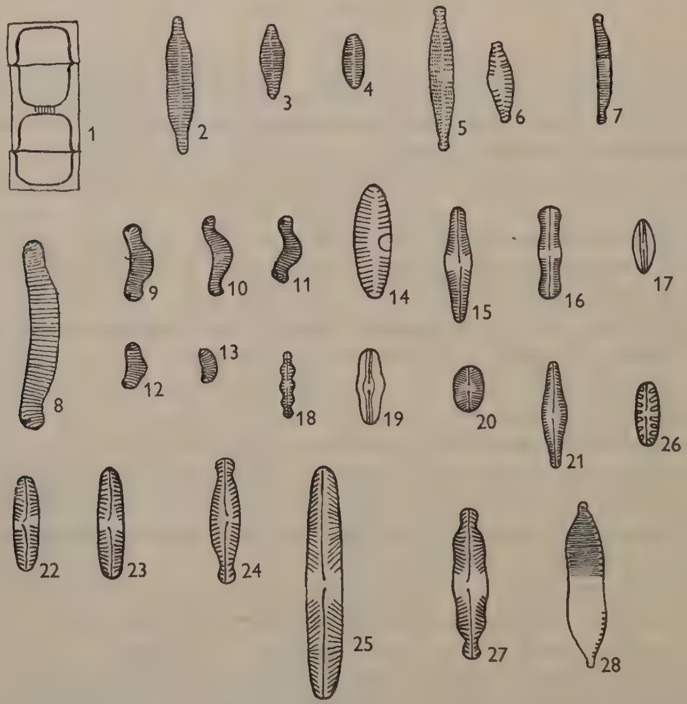
The samples were all treated with a mixture of sulphuric and nitric acids, washed, and the residual diatom frustules mounted in Sirax.

The majority of the species found appear to be highly characteristic of such Bryophyte communities. The small number of species in this community is no doubt a reflexion of the extreme conditions imposed by the aerial habitat. In addition, a size limitation is obvious, for although occasional 60μ long frustules of *Pinnularia viridis* were found (which is small for this species), the vast majority of species, and all the dominants, have cells less than 20μ in length. Some species are so small (up to 5μ in length) that their identification is difficult, and hence all the common forms are illustrated in Figs. 1–28. Petersen (1915), Beger (1927, 1928), Lund (1946) and Brendemühl (1949) comment on a similar size restriction of soil diatoms.

Samples II and VI (Table 1) were very poor in species and also in numbers of frustules present, since no forms can be ranked as frequent or common. The samples were obtained from very small thread-like Hepaticae—*Cephalozia* and *Calypogeia* which would thus appear to be unfavourable habitats for diatoms. Of the remaining samples the richest in epiphytes is *Eurhynchium praelongum* followed by samples I (*Lophocolea*), IV (*Pellia*) and V (*Pellia*+*Cephalozia*), all having a similar number of species. Although the dominants vary somewhat with the samples, the general overall impression of the flora is that its major components are *Melosira dickiei*, *Fragilaria virescens*, *Eunotia exigua*, *Navicula perpusilla*, *N. indifferens*, *Pinnularia microstauron* fo. *diminuta* and *Hantzschia amphioxys*.

That this is a true aerial epiphytic community and not an extension of the soil-living community is seen, if comparison is made between the species list on p. 659 with those for soil diatoms in Petersen (1915), John (1942) and Lund (1946). Only one of the present common species was recorded by Petersen (1915) this being *Melosira dickiei*, found once and then amongst moss and thus only included tentatively in Petersen's list. Only two of my rarer species are common to both communities.

Petersen (1915) comments on the fact that the soil diatoms almost all belong to the suborder Raphidineae of the pennate diatoms. This, however, does not apply to the Bryophytic flora since *Fragilaria* and *Eunotia* belong to the Araphidineae and Raphidioideae respectively, and *Melosira* to the Centrales. These three are amongst the most abundant and characteristic genera of this habitat and thus Petersen's comment on 'aerofiles' does not hold good for the aerial epiphytes. Motility is thus not such a vital requisite in this as in the soil community.



Figs. 1–28. 1. *Melosira dickiei*; 2, 3, *Fragilaria virescens*; 4, *F. virescens* var. *elliptica*; 5, 6, *F. intermedia*; 7, *Eunotia tenella*; 8, *E. pectinalis* var. *minor*; 9–13, *E. exigua*; 14, *Achnanthes lanceolata* var. *elliptica*—rapheless frustule; 15, *Stauroneis muriella*; 16, *Navicula contenta*; 17, *N. indifferens*; 18, *N. söhrensis*; 19, *N. perpussila*; 20, *N. seminulum*; 21, *Pinnularia irrorata*; 22, 23, *P. microstauron* fo. *diminuta*; 24, *P. globiceps* var. *krookii*; 25, *P. intermedia*; 26, *P. balfouriana*; 27, *P. mesolepta*; 28, *Hantzschia amphioxys*, only terminal striations drawn. All × 800.

Many of the Diatoms in Table 1 extend from this aerial habitat into completely aquatic habitats and only very few can be said to be more common on the land. Of the dominant forms, *Melosira dickiei*, *Navicula indifferens*, *N. perpusilla* and of the less common forms, *N. contenta*, *N. söhrensis* and *Pinnularia balfouriana* may be said to be most commonly encountered as Bryophyte epiphytes. Comments on habitats in the diatom floras indicate that of these the small *Navicula* species are also common on very wet rock faces. However, amongst the dominants the present author has only found *Fragilaria virescens* in any quantity in a purely aquatic habitat (calcareous stream).

Comparison of the aerial Bryophyte community with that of submerged Bryophytes (Round, in preparation and unpublished data) shows little similarity, e.g. on *Fontinalis* in Malham Tarn, Yorkshire, the dominants are *Achnanthes*, *Cymbella*, *Cocconeis*, *Tabellaria* and *Denticula* and in streams at Leuknor, Buckinghamshire, *Achnanthes*, *Nitzschia* and *Diploneis ovalis* var. *oblongella*. None of these genera is at all common in aerial Bryophyte collections. The exceedingly common *Epithemia–Cymbella–Gomphonema–*

Table 1. *The distribution of diatom species in the samples*
(C = common, F = frequent, O = occasional, + = present.)

	I	II	III	IV	V	VI
Melosira dickei (Thwait.) Kütz.	C	+	F	O	C	.
Fragilaria virescens Ralfs	F	.	.	.	O	.
F. virescens var. *elliptica* Hust.	+	.	+	.	.	.
F. intermedia Grun.	.	.	+	F	F	+
Eunotia pectinalis (Kütz.) Rabenh.	+	.	+	+	+	.
E. pectinalis var. *minor* (Kütz.) Rabenh.	+	.	+	.	.	.
E. exigua (Bréb.) Grun.	.	.	C	C	+	.
E. lunaris var. *subarcuata* (Naeg.) Grun.	+	.	.	.	.	.
E. tenella Grun.	.	.	+	.	.	.
Cocconeis placentula Ehr.	.	.	+	.	.	.
Achnanthes lanceolata Bréb.	+	.	+	+	+	.
A. lanceolata var. *elliptica* Cleve	.	.	+	.	.	.
Stauroneis muriella Lund	+	.	+	+	+	.
Diploneis ovalis (Hilse) Cleve	.	.	+	+	.	.
Navicula contenta Grun.	.	.	+	+	.	.
N. perpusilla Grun.	O	.	F	O	.	.
N. indifferens Hust.	.	.	F	C	.	.
N. atomus (Naeg.) Grun.	.	.	.	.	+	.
N. söhrensis Krasske	O	.	+	+	O	.
N. cocconeiformis Grég.	+	.	+	+	C	+
Pinnularia intermedia (Lagerst.) Cleve	+	.	.	.	.	.
P. microstauron fo. *diminuta* Grun.	F	+	C	C	C	+
P. mesolepta (Ehr.) W. Sm.	+	.	.	+	.	.
P. globiceps var. *krookii* (Grun.) Cleve	.	+	+	.	+	.
P. irrorata (Grun.) Hust.	.	.	+	.	.	.
P. balfouriana Grun.	+	.	.	+	.	.
P. viridis (Nitzsch) Ehr.	+	.	+	.	+	.
Hantzschia amphioxys (Ehr.) Grun.	F	.	+	.	+	.
Nitzschia frustulum (Küst.) Grun.	.	.	+	+	+	.
	17	3	23	16	15	3

Achnanthes complex, epiphytic on water plants, is completely absent from this aerial epiphytic community.

In Beger's (1927) account the samples from the Elbsandsteingebirges are of greatest comparative interest. The species occurring in 50 % or more of these samples are *Eunotia bigibba*, *E. lunaris*, *Melosira dickiei*, *Pinnularia borealis*, *Eunotia exigua*, *Fragilaria virescens*, *Melosira roseana*, *Microneis* (now *Achnanthes*) *minutissima* and *Navicula contenta*. Of these only three occur in my list of major species in the Brotherton Park samples and only one other in the total number found. Of the less frequent species in the Elbsandsteingebirges none occurs in Brotherton Park. The other lists given by Beger of epiphytes attached to Bryophytes growing on well walls, trees, etc., show even fewer species to be common to the two regions. However, the species of Beger's and my investigations are frequently very closely related and also similarly small in size. Further comment on the presence or absence of species in the two regions occurs in the notes (p. 660–61).

Hustedt (1942) published an account of diatoms from some Bryophyte samples in which he recorded a total of 147 species or varieties. However, such large numbers were not recorded in all samples, e.g. nos. 2, 3, 4, contain 39, 12 and 22 forms respectively, whilst nos. 1, 2, 5, 6, 7, contain 46, 39, 76, 85 and 65 respectively. This difference is attributed by Hustedt to the distance from a body of water. Indeed, very many of the 147 forms recorded by Hustedt are also commonly found in free water and therefore not truly characteristic of the land Bryophyte flora. In this same paper Hustedt comments on the greater number of species encountered in the last three samples from alkaline soils as opposed to the first two from acid. Thus the epiphytic Bryophyte flora appears to be affected by pH of the soil as do the soil diatoms (Lund, 1946; Brendemühl, 1949).

Beger (1927, 1928) divided the epiphytic diatom community on Bryophytes into 'xerotisch', 'mesophilisch' and 'hydrotisch' types. Clearly the Brotherton Park samples must be included in the latter on habitat considerations. Also Beger (1928) characterized the 'xerotisch' type by *Pinnularia borealis*, *Hantzschia amphioxys*, *Melosira roeseana* and *Achnanthes coarctata*, only one of which occurs frequently in one sample (and rarely in two others), whilst the others are absent. Typical of his 'hydrotisch' type are *Melosira dickiei*, *Tetracyclus braunii*, *Denticula elegans*, *D. tenuis*, *Grunowia sinuata*, *Navicula perpusilla*, *N. roteana*, *N. atomus*, *Pinnularia brebissonii*, *Eunotia* spp. and *Cymbella* spp. Again only a small number of these species occur in the Brotherton Park samples, possibly due to the fact that Beger's collections were from calcareous alpine regions.

Beger (1928) mentions three species amongst others, *Pinnularia borealis*, *Hantzschia amphioxys* and *Navicula mutica*, which he regards as characteristic species of the Bryophyte community. These three are, however (unlike such equally characteristic species as *Melosira dickiei*, *M. roeseana* and *Achnanthes coarctata*), very common in soils (John, 1942; Lund, 1946; Brendemühl, 1949, etc.). Although recorded by Hustedt (1942), they are not at all common or characteristic of his samples and only one, *Hantzschia amphioxys*, has been recorded by the present author. Thus the possibility does arise that the true moss diatoms are very few indeed, and it does point to the great importance of exclusion of soil particles from the samples.

Hustedt (1942) comments on the occurrence of many so called 'nordisch-alpin, tropisch oder halophil' species in Bryophyte samples. These habitats, together with that of the aerial Bryophytes, have one striking feature in common, i.e. the subjection of the communities to periodic or perpetual drought, either actual or physiological. The ability of the Bryophyte diatoms to withstand prolonged drought has been shown by Beger (1927).

NOTES ON SOME OF THE SPECIES

Melosira dickiei (Thwait.) Kütz. is, according to the floras, rather uncommon and confined to wet moss habitats. Of all the species recorded in these Bryophyte samples *M. dickiei* appears to be confined to this community. Illustrations of this species rarely show the punctation of the cell membrane, but this can be clearly seen in some of the Brotherton Park samples (see Fig. 1). Formation of inner frustules was not noted in these samples. Unexpectedly, the common moss-dwelling *M. roeseana* was not recorded.

Fragilaria virescens Ralfs occurs rarely in lakes and in streams, but is fairly common in Beger's (1927) samples. Elsewhere the author has only once found it in quantity and then as an epiphyte on *Cladophora* in a stream.

Eunotia. Apart from *E. exigua* the species of this genus found in these samples also occur in aquatic habitats. It is common in Beger's material and is probably to be regarded as highly characteristic of the habitat.

Cocconeis placentula Ehr. Probably not a true component of this flora, being much more common in aquatic habitats.

Achnanthes lanceolata Bréb., is, according to Beger, more common in the dryer moss communities. On the other hand, it has been recorded by the author in great abundance as a stream epiphyte. Beger also records *A. minutissima*, *A. exigua* and *A. coarctata* in moss samples, none of which have appeared in these samples. However, several other very small *Achnanthes* species (or *Navicula*) have been noted but, due to lack of distinguishing characters, undetermined.

Diploneis ovalis (Hilse) Cleve, see comment re *Cocconeis*.

Navicula indifferens Hust. This very small form with no striations visible was first recorded from Bryophyte samples by Hustedt (1942). It is very close to *N. krasskei* Hust. but is smaller and the depressions on either side of the axial area seem to be absent.

N. cocconeiformis Greg. Frustules of this species were observed, often much smaller than the size limits given in Hustedt (1930).

Pinnularia intermedia (Lagerst.) Cl. was recorded by Hustedt (1942) on Bryophytes but is also common in soils (Lund, 1946).

P. microstauron fo. *diminuta* Grun. The very common diatom illustrated in Figs. 22 and 23 seems to be nearest to this form recorded from soils by Lund (1946).

P. irrorata (Grun.) Hust. The specimens recorded in these observations seem to agree best with the illustrations of Hustedt (1942). My fig. 21 shows a specimen which is without a wide central area reaching either side of the frustule—this must, I think, be included in the species.

P. balfouriana Grun. The small *Pinnularia* frustules found in these samples and obviously belonging to the section Distantes, probably belong to this species. Beger (1927, 1928), however, records the closely related species *P. borealis* Ehr. as one of the dominant forms present in almost all Bryophyte samples. However, Beger (1927) gives a table of the size variations of a large number of *P. borealis* frustules, none of which are less than 20μ in length. Thus, although the habitat does restrict the size limits of species there can be little doubt that the present record is of *P. balfouriana* due to its extremely small size. Also the habitat is in agreement with that given by Hustedt (1930).

Hantzschia amphioxys (Ehr.) Grun. is recorded by Beger (1927, 1928) and Hustedt (1942) in Bryophyte samples. The frustules common in sample I from Brotherton Park are small and have more striae than given in Hustedt (1930).

Summary

The diatom flora growing on Bryophytic material on wet rock in Brotherton Park, Cheshire has been investigated. In all, twenty-nine species were found. Comparison of this community with that of soils and permanently submerged Bryophyta suggests that it is independent and highly characteristic in its species composition. Notes are given on some of the most interesting species.

I wish to thank Dr J. W. G. Lund for his valuable comments on the manuscript.

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A note on some diatom communities in calcareous springs and streams.

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(Communicated by Dr J. W. G. Lund, F.L.S.)

(With one Text-figure)

[Read 24 May 1957]

In 1954 eighteen samples of diatoms were collected from springs and streams used as watercress beds lying at the foot of chalk hills, at Leuknor in Buckinghamshire. Sediments and plant material were taken from these habitats.

Three springs were visited; two of these were in small sheltered hollows devoid of aquatic higher plants, whilst the third was a larger, diffuse region in a small pond filled with watercress. Samples 1–3 were sediments taken respectively from each of these springs near the upwelling points. From the first spring, sample number 6 of *Batrachospermum* was collected, from the second, sample 4 of *Fontinalis* and 5 of *Batrachospermum* and from the third, watercress sample number 9. The remaining eleven samples were taken from the streams arising from the springs from which samples 1 and 2 were taken. Numbers 7 and 8 were scrapings from stones, 10–14 were epiphyte collections from *Ranunculus*, *Lemna*, *Cladophora*/*Vaucheria*, *Cladophora* and *Fontinalis* respectively, and samples 15–18 were stream sediments.

The complete analysis of the diatoms in these samples is given in Table 1.

Table 1. *The distribution and abundance of diatom species in the Leuknor streams and springs*

(A = abundant, VC = very common, C = common, F = frequent, O = occasional, + = present.)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Melosira varians Ag.	.	.	+	.	.	.	.	.	.	C	+	+	+	+	O	O	+	+
M. arenaria Moore	.	+	·	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cyclotella meneghiniana Kütz.	.	.	.	.	.	.	.	.	.	C	+	O	.	.	O	+	.	+
Tabellaria flocculosa (Roth) Kütz.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Meridion circulare Ag.	+	+	C	+	.	.	+	.	C	+	+	C	F	+	+	+	+	+
Fragilaria capucina Desm.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	.
F. intermedia Grun.	+	.	C	.	.	.	.	.	+	VC	C	C	F	+	F	+	+	+
F. harrissonii W. Sm.	+	C	+	+	+	.	.	+	.	O	.	C	.	.	+	+	.	+
F. harrissonii var. *rhomboides* Grun.	.	+	+	.	.	.	.	.	+	+	+	+	.	.	+	+	.	+
F. construens (Ehr.) Grun.	.	.	.	.	+	.	.	.	+	.	.	+	+	.	.	.	.	+
F. virescens Ralfs	.	.	C	.	.	.	.	.	C	.	.	.	C	.	.	.	+	C
F. brevistriata Grun.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Synedra ulna (Nitzsch) Ehr.	+	+	+	+	+	+	+	.	C	A	C	O	C	.	C	F	+	O
S. ulna var. *danica* (Kütz.) Grun.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.
S. amphicephala Kütz.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.
S. vaucheriae Kütz.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
S. parasitica var. *subconstricta* Grun.	O	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	
Eunotia pectinalis (Kütz.) Rabenh.	.	.	.	.	+	.	.	.	.	+	+	.	.	C	.	.	+	.
E. pectinalis var. *minor* (Kütz.) Rabenh.	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.
E. lunaris var. *subarcuata* (Naeg.) Grun.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Cocconeis pediculus Ehr.	.	.	.	.	.	.	.	.	.	O	C	.	.	.	.	.	.	.
C. placentula Ehr.	+	+	+	+	+	.	.	+	O	+	C	+	+	O	.	.	+	+
C. placentula var. *euglypta* (Ehr.) Cleve	+	+	+	C	.	.	.	+	.	+	C	O	.	C	.	.	+	+
C. diminuta Pant.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Achnanthes microcephala Kütz.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
A. minutissima var. *cryptocephala* Grun.	.	.	.	+	+	.	.	.	F	.	.	.	.	.	.	.	.	.
Achnanthes exilis Kütz.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
A. affinis Grun.	.	.	.	+	C	+	.	.	C	.	+	+	+	C	.	.	.	+
A. hungarica Grun.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
A. exigua Grun.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
A. exigua var. *heterovalvata* Krasske	C	C	.	.	.	.	.	.	+	.	.	+	+	+	.	.	.	

Table 1 (*cont.*)

(A=abundant, VC=very common, C=common, F=frequent, O=occasional, +=present.)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
. *hauckiana* Grun.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *grimmei* Krasske	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
. *lanceolata* Bréb.	C	C	A	A	O	+	O	O	A	C	C	A	A	A	C	O	+	C
. *lanceolata* var. *elliptica* Cleve	C	VC	A	C	C	+	O	O	A	+	O	C	A	C	C	+	+	C
hoicosphenia curvata (Kütz.) Grun.	+	+	+	.	.	+	+	.	.	+	.	C	.	+	.	.	.	.
rustulia vulgaris Thwaites	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
yrosigma acuminatum (Kütz.) Rabenh.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.
aloneis silicula (Ehr.) Cleve	+	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+
. *schumanniana* var. *biconstricta* Grun.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
eidium affinis var. *amphirhynchus* (Ehr.) Cleve	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.
. *iridis* fo. *vernalis* Reichelt	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
. *productum* (W. Sm.) Cleve	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
. *dubium* (Ehr.) Cleve	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
iploneis ovalis (Hilse) Cleve	+	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	+
. *ovalis* var. *oblongella* (Naeg.) Cleve	.	.	.	.	.	.	.	.	+	.	.	.	.	C	.	.	.	+
. *puella* (Schaumann) Cleve	+	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+
tauroneis phoenicentron Ehr.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *anceps* Ehr.	+	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
. *smithii* Grun.	O	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+
nomoeoneis exilis (Kütz.) Cleve	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
avicula cuspidata Kütz.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
. *mutica* Kütz.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *mutica* var. *binodis* Hust.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *mutica* var. *nivalis* (Ehr.) Hust.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *binodis* Ehr.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
. *bacillum* Ehr.	O	O	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
. *pupula* Kütz.	+	+	+	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.
. *pupula* var. *capitata* Hust.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+
. *cryptocephala* Kütz.	+	.	+	.	.	.	.	.	.	+	.	.	.	+	+	.	+	+
. *hungarica* var. *capitata* (Ehr.) Cleve	O	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
. *radiosa* Kütz.	+	+	.	.	.	.	.	.	.	C	+	+	.	+	+	+	.	+
. *gracilis* Ehr.	.	.	.	+	+	.	.	.	.	O	.	.	.	+	.	.	.	.
. *peregrina* var. *kefvingensis* (Ehr.) Cleve	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *menisculus* Schumann	O	+	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	+
. *dicephala* (Ehr.) W. Sm.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *placentula* fo. *rostrata* A. Mayer	+	+	F	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
. *placentula* fo. *jenisseyensis* (Grun.) Meister	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
. *exigua* (Greg.) O. Müll.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+
. *oblonga* Kütz.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.
. *pygmaea* Kütz.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.
innularia leptosoma Grun.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *mesolepta* (Ehr.) W. Sm.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.
. *microstauron* (Ehr.) Cleve	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
. *divergens* W. Sm.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
. *borealis* Ehr.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *major* (Kütz.) Cleve	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *viridis* (Nitzsch) Ehr.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.
mphora ovalis Kütz.	+	+	+	.	.	.	+	.	.	.	.	.	.	+	.	.	+	+
mphora ovalis var. *libyca* (Ehr.) Cleve	F	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
. *ovalis* var. *pediculus* Kütz.	F	C	.	.	+	.	+	+	+	+	+	+	.	C	+	+	.	.
. *veneta* Kütz.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ymbella cesati (Rabenh.) Grun.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
. *naviculiformis* Auerswald	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.
. *prostrata* (Berkeley) Cleve	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
. *ventricosa* Kütz.	.	+	.	.	+	.	.	.	.	+	+	.	.	.	+	+	.	.
. *affinis* Kütz.	+	+	.	.	.	.	.	.	.	+	+	.	.	.	.	C	+	+
omphonema acuminatum Ehr.	+	+	+	.	+	.	.	.	.	+	.	+	+	.	.	.	+	+
. *acuminatum* var. *coronatum* (Ehr.) W. Sm.	+	.	.	.	.	.	.	.	+	+	.	+	.	+	.	.	.	.
. *acuminatum* var. *brebissonii* (Kütz.) Cleve	.	.	.	+	.	.	.	.	+	+	+	.	.	+	.	.	.	.
. *acuminatum* var. *trigonocephalum* (Ehr.) Grun.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
. *parvulum* (Kütz.) Grun.	+	.	.	.	+	.	.	.	+	+	.	O	+	+	.	.	+	.
. *parvulum* var. *micropus* (Kütz.) Cleve	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.
. *angustatum* (Kütz.) Rabenh.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
. *intricatum* var. *pumilum* Grun.	A	O	.	+	.	.	A	A	.	.	+	.	.	.	.	+	.	.
. *constrictum* Ehr.	.	.	+	.	.	.	.	.	+	C	+	+	+	+	+	+	+	+
. *olivaceum* (Lyngb.) Kütz.	+	.	.	.	.	.	.	.	.	C	.	.	.	.	+	+	.	.
. *olivaceum* var. *minutissimum* Hust.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.

Table 1 (*cont.*)

(A=abundant, VC=very common, C=common, F=frequent, G=occasional, +=present.)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
G. olivaceum var. *calcareum* Cleve	.	.	.	.	.	.	.	.	.	C	+	.	.	+	.	+	+
Denticula tenuis Kütz.	+	A	.	+	A	.	+	+	.	C	F	+	.	.	F	C	.
Epithemia zebra var. *saxonica* (Kütz.) Grun.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
E. turgida (Ehr.) Kütz.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
E. turgida var. *granulata* (Ehr.) Grun.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
E. hyndmanni W. Sm.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.
Hantzschia amphioxys (Ehr.) Grun.	O	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Nitzschia hungarica Grun.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
N. angustata (W. Sm.) Grun.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+
N. angustata var. *acuta* Grun.	O	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
N. dissipata (Kütz.) Grun.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	C
N. amphibia Grun.	+	.	.	.	.	.	+	+	.	+	+	+	C	+	.	.	.
N. frustulum var. *perpusilla* (Rabenh.) Grun.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
N. perminuta Grun.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.
N. dubia W. Sm.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
N. fonticola Grun.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
N. palea (Kütz.) W. Sm.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	A	+
N. sigmoidea (Ehr.) W. Sm.	.	+	C	+	.	.	.	.	+	+	+	+	.	.	+	+	A
Cymatopleura solea (Bréb.) W. Sm.	+	+	+	.	.	.	.	.	.	+	.	.	.	.	.	.	+
C. elliptica (Bréb.) W. Sm.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+
Surirella linearis var. *helvetica* (Brun.) Meister	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S. angustata Kütz.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+
S. tenera Greg.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S. ovata Kütz.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+
S. ovata var. *pinnata* (W. Sm.) Hust.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Total	72	33	33	19	18	6	12	10	20	44	31	39	18	25	24	22	50

In this small area of springs and streams a total of 123 species of diatoms have been recorded, of which the most widespread are *Meridion circulare*, *Synedra ulna*, *Cocconeis placentula* and var. *euglypta*, *Achnanthes lanceolata* and var. *elliptica*, followed by *Fragilaria intermedia*, *F. harrissonii*, *Amphora ovalis* var. *pediculus* and *Denticula tenuis*. These are all attached forms, which is not surprising since all samples are from running water. The number of species at the sampling stations is very variable. The epilithic and epiphytic communities in the springs are very poor in species. However, the former are rich in cells of a single species (*Gomphonema intricatum* var. *pumilum*), whereas the latter are characterized by a very sparse population (especially so on *Batrachospermum*). The largest number of species obtained from any one station was seventy-two (sample 1), but the springs are not all equally rich. One other station approaches this number and that is a stream sediment with fifty species (sample 17) which has a typical sediment flora in contrast to the other stream samples which are dominated by attached forms. The truly epiphytic samples from the streams are midway in number of species between the two rich sediments and the samples poor in species from stones and springs.

Sediment flora of the springs. The dominant species in the springs are *Achnanthes lanceolata* and var. *elliptica* (these being the only dominant forms common to all three), *Gomphonema intricatum* var. *pumilum*, *Achnanthes exigua* var. *heterovalvata*, *Denticula tenuis*, *Amphora ovalis* var. *pediculus*, *Nitzschia sigmoidea*, *Fragilaria intermedia*, *F. virescens* and *Meridion circulare*. The last four occur only in sample 3, which is overgrown with watercress and may therefore not be characteristic of the sediments of springs. The following are common to all three springs: *Meridion circulare*, *Fragilaria harrissonii*, *Synedra ulna*, *Cocconeis placentula* and var. *euglypta*, *Achnanthes lanceolata* and var. *elliptica*, *Rhoicosphenia curvata*, *Navicula bacillum*, *N. pupula*, *N. placentula* fo. *rostrata*, *Amphora ovalis*, *Gomphonema acuminatum*, *Nitzschia dissipata* and *Cymatopleura solea*. Since this list of species common to all three springs contains but three of the dominant species, the difficulty of characterizing this type of spring flora is clear. A combination of the two lists may be necessary, but how accurately this represents the diatom flora of calcareous springs will only be revealed by sampling a larger number.

Among interesting species occurring is *Melosira arenaria* (in sample 2) which is derived no doubt from the *Fontinalis* growing here (sample 4). This is a somewhat rare species which appears to be confined to highly calcareous waters in this country. It has also been recorded from late glacial lake sediments (Round, 1957), and Cleve (1895) comments on its occurrence in similar habitats in Sweden. It is probably associated with aquatic Bryophytes when growing in such places. The presence of *Navicula mutica* and its varieties in sample 1 is noteworthy, for normally this species is uncommon in purely aquatic habitats but frequent in soils. Only further investigation will show whether this is a true extension of its habitat or merely the result of contamination from the soil around the spring (cf. the presence of the common soil diatom *Pinnularia borealis*).

Epiphyte flora of the springs. No higher plants were found growing in these springs (the watercress around sample 3 was not growing where the water was upwelling), and hence the epiphytes are derived from the moss *Fontinalis* and the Rhodophycean alga *Batrachospermum*, a frequent colonizer in springs. The sparsity of attached diatoms on the latter plant is almost certainly due to the copious production of mucilage. The *Fontinalis* flora is dominated by *Achnanthes lanceolata* with *A. lanceolata* var. *elliptica*, *Cocconeis placentula* var. *euglypta*, *Melosira arenaria* and *Epithemia hyndmanni*. The occurrence of *Melosira arenaria* and *Epithemia hyndmanni* together is of great interest since they have also been found associated in late glacial Kentmere lake samples (Round, 1957). Only the first of the two *Batrachospermum* samples contained sufficient cells to enable any estimate of frequency to be made. This clearly showed that there was a single dominant in the flora, *Denticula tenuis* (also common on the sediments of this spring, see above). Of secondary importance here are *Achnanthes lanceolata* and var. *elliptica*, *A. grimii* and *A. affinis*. All these are very minute linear species which presumably can attach themselves to the mucilaginous thallus of the *Batrachospermum*.

Epilithic samples. The diatoms form a thick brown coating on the stones in the streams. This flora is characterized by: (1) the great paucity of species (10 and 12); (2) the dominance at both stations of *Gomphonema intricatum* var. *pumilum*; (3) the presence in small numbers of *Achnanthes lanceolata* (together with var. *elliptica*), the rest being rare. These features clearly segregate this community from that on plant material in the streams and support my view (Round, 1956) that the epilithic community should be regarded as separate from the epiphytic. The lack of contamination of the epilithic flora by the bottom-living forms is remarkable; only two species are recorded here which belong to the sediment flora (*Neidium affine* var. *amphirhyncus* and *Amphora ovalis*).

Epiphytic communities. Contrasted with that on stones, the epiphytic flora is composed of a larger number of species and, although no single one is dominant, several are common. The most common species, however, show a striking uniformity; thus, the epiphytic samples are dominated by *Achnanthes lanceolata* (including var. *elliptica*) and *Synedra ulna*. Also common in the higher plant samples are *Cocconeis placentula* and var. *euglypta*, *Fragilaria intermedia*, *F. virescens*, *Achnanthes affinis*, *Meridion circulare* *Gomphonema constrictum*, *G. olivaceum* and var. *calcarea*, *Denticula tenuis*, *Navicu* *radiosa* and *Melosira varians*. The latter five forms are present on the *Ranuncul* sample, which is noteworthy in having the largest number of common species and largest total number of species amongst the epiphyte samples. This is an excellent exam of the effect of the habitat on the composition of the community. The much divided affords an excellent habitat for the epiphytes (cf. that of *Myriophyllum* and *C* *phyllum*) compared, for example, with the habitat afforded by the under surf floating *Potomageton* leaves.

Although the dominant epiphytic diatoms are the same in the *Cladophora* and *nalis* samples, the remaining common species are somewhat variable, e.g. in sa *Meridion circulare*, *Fragilaria intermedia*, *F. harrissonii*, *Achnanthes lanceol* *elliptica* and *Rhoicosphenia curvata*, in sample 13 only *Synedra ulna* and *Fr*

T

virescens, and in sample 14 *Cocconeis placentula* var. *euglypta*, *Achnanthes affinis*, *A. lanceolata* var. *elliptica*, *Amphora ovalis* var. *pediculus*, *Nitzschia amphibia*, *Diploneis ovalis* var. *oblongella*, *Eunotia pectinalis* and var. *minor*. Although containing some of the same common forms encountered as epiphytes of higher plants, there are notable differences such as the complete absence of *Gomphonema* and *Denticula* in the algal mats.

There are several marked differences between the epiphytic flora and that of the springs and stones. The filamentous diatom *Melosira varians* is more frequent here and also in the stream sediment samples. *Cyclotella meneghiniana* is typical of the stream plankton, and although present is doubtless a contaminant here and in the samples. *Cocconeis pediculus* is found in only two of the epiphyte samples and thus, in agreement with its general distribution, is here more restricted than the closely related *C. placentula*. *Navicula pygmaea*, which is normally a brackish-water form, is recorded in the epiphyte and stream samples. The previously common *Gomphonema intricatum* var. *pumilum* now gives way to other *Gomphonema* species such as *G. parvulum*, *G. constrictum* and the forms of *G. olivaceum*.

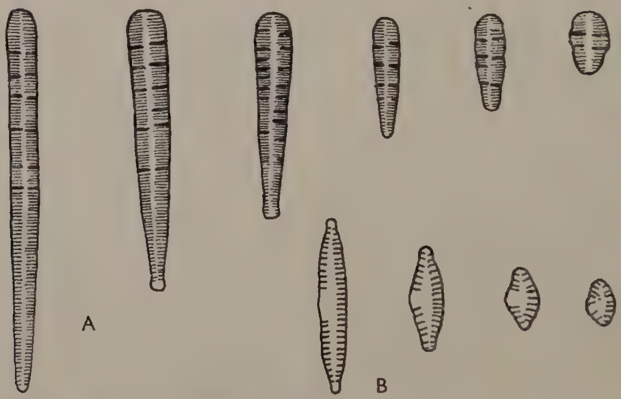

Fig. 1. The size variation of *Meridian circulare* (A) and *Fragilaria intermedia* (B). ×800.

Stream sediments. Apart from sample 17, these do not possess a true bottom-living diatom flora as, for instance, do streams in Worcestershire (Round, work in progress). Instead the flora consists of forms commonly found as epiphytes, the dominants being *Achnanthes lanceolata* and var. *elliptica* in sample 18, and these two plus *Synedra ulna* in sample 15. Less common in 18 are *Nitzschia sigmoidea*, *Fragilaria virescens* and *Synedra ulna*. Only one species, *Nitzschia sigmoidea*, can be regarded as truly bottom-
iving; this is indeed the dominant and only common form in sample 17. Sample 16
ay be regarded as having a true bottom flora, since its dominant species is *Nitzschia*
lea. However, the common *Denticula tenuis* and *Cymbella affinis* are probably not
bottom forms and, in addition, the total species list of this sample is small, con-
ing few diatoms characteristic of sediments. On the other hand, the rich sample 17
ins many species belonging to the genera *Navicula*, *Pinnularia*, *Neidium*, *Nitzschia*
ymatopleura which are typical of sediments. This feature alone separates sample 17
he other sediments and characterizes the habitat as being particularly favourable
bottom-living community (cf. sample 10 with its large number of species and
v also sample 1). There is no obvious reason for the lack of such a flora at the
ree stations. However, the possibility must be borne in mind, remote as
r it to be, that the epiphytic forms found in abundance on these three sediments
t living attached to the sediment itself. A point of interest is that the plank-
cies *Cyclotella meneghiniana* is absent from sample 17, but present on the three

other sediments, which suggests that these were obtained from stations at which sedimentation of diatoms was occurring.

A striking feature of the diatom flora in these springs and streams is the extreme range of size shown by some of the species, often within a single sample. Examples of this are illustrated in Fig. 1 by *Fragilaria intermedia* and *Meridion circulare*. A notable feature of these is that the shortest cells are actually broader than the larger. Such cells in *Fragilaria intermedia* are often abnormal in shape and markings.

Discussion

Floristically the Leuknor streams bear a certain resemblance to alkaline streams in Funen, Denmark (Foged, 1947–9). Many of the dominants in the Danish streams were also attached forms although, since no precise data on habitats are given, it is difficult to make direct comparisons. Points of interest, however, are the common occurrence in these Danish streams of *Melosira granulata* (Ehr.) Ralfs. and its varieties, *Thalassiosira fluviatilis* Hust. and *Cyclotella comta* (Ehr.) Kütz., all of which are absent from the Leuknor samples. The common *Fragilaria* spp. in the present samples are not those of the Funen streams, although this genus is well represented. Butcher (1946) records similar dominants in highly calcareous streams, e.g. *Fragilaria intermedia*, *F. leptostauron*, *Cocconeis placentula*, *Achnanthes minutissima*, *A. linearis*, *A. lanceolata*, *Navicula cryptocephala*, *N. viridula*, *Cymbella ventricosa*, *Gomphonema parvulum*, *G. constrictum*, *G. olivaceum*, *Nitzschia palea* and *N. acicularis*. Here again the species of the Funen streams mentioned above are absent. Compared with the Worcestershire streams (work in progress) the bottom samples from Leuknor show a very poor flora on the sediments and nowhere in Worcestershire have attached forms been predominant. This strongly suggests that such samples were taken from regions of sedimentation and their interest lies in the inability of the typical bottom-living community to develop in such stretches or perhaps on a sediment composed of dead frustules.

The presence of *Navicula pygmaea* is interesting, for this species normally occurs in saline waters. However, in Worcestershire it has also been recorded in streams of low chloride content. It seems probable that a high concentration of other salts can replace chlorides in the habitat without eliminating this species.

The spring samples show some similarities with those from the alkaline Balkan region investigated by Hustedt (1945) where, around Lake Ochrida, *Achnanthes lanceolata*, *A. exigua* var. *heterovalvata* (particularly on mosses in the springs), *Amphora ovalis* var. *pediculus*, *Caloneis bacillum* and *Cocconeis placentula* var. *euglypta* are common. With the exception of *Caloneis bacillum* these are also common forms in the Leuknor springs. Also in Hustedt's (1945) samples are *Melosira arenaria*, again on moss material in the springs and *Hantzschia amphioxys*; this latter is probably associated with the moss material rather than the spring. It is indeed difficult to point to any element of the flora which could be considered to be a 'spring' form. Instead, the list of species common to all three springs contains eight which are commonly found as attached epiphytes in running waters and seven which occur both on stream, pond or lake sediments. The habitat afforded by the sediments in the springs is probably best thought of as a sediment of running water with certain peculiar features such as constant temperature, aeration, chemical composition, etc. Possibly it is the constant disturbance of the particles with the subsequent elimination of silting which allows the attached element of the flora to colonize sediments.

Cholnoky (1933–4) found that *Denticula elegans* was the dominant species in a spring in Hungary, and also present were *Synedra amphicephala*, *Anomoeoneis exilis*, *Navicula falaisensis* var. *lanceolata*, *N. seminulum* (a common form in springs around Budapest according to Cholnoky), *N. subtilissima*, *Gomphonema longiceps* var. *subclavata*, *Cymbella cesatii*, *C. laevis*, *C. brehmii* and *C. bohemicum*. Cholnoky states that *Achnanthes* *lanceolata*, one of the dominant species in the Leuknor region, is a species rare in waters of low organic matter content and low temperature. Neither of these features could be said to characterize the Leuknor spring samples where this species is abundant. The present findings are in complete agreement with Hustedt (1930) with whom Cholnoky disagrees over this point.

SUMMARY

The diatom floras of some calcareous spring and stream samples in a small watercress-growing area have been examined. Plants and sediments from the springs, and plants, sediments and stones from the streams have yielded a total of 123 diatoms, divisible into distinct communities, the composition of which is discussed. The sediments yield a large number of species with several species co-dominant. The epilithic samples are poor in species with generally a single dominant. The Rhodophycean alga *Batrachospermum* supports a very sparse epiphytic flora, whereas that on mosses, in algal felts and on water plants is richer. Comparison is made with data from Denmark, Hungary and the Balkans.

The author wishes to thank Dr J. Tomlinson for introducing him to this interesting area and to Dr J. W. G. Lund for his criticism of the manuscript.

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Leuco-anthocyanins. 3. The nature and systematic distribution of tannins in dicotyledonous plants.

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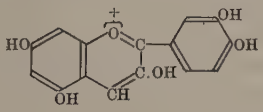
[Read 24 May 1957]

It was recently observed by Bate-Smith & Lerner (1954) that leuco-anthocyanins, a class of compounds notable for their ability to produce anthocyanidins when boiled with mineral acids, showed a considerable degree of correlation in their distribution with that of the botanical tannins, as recorded by Metcalfe & Chalk (1950). The question to be discussed in this paper is how frequently in fact they may be responsible for the recorded occurrence of tannins in the botanical literature.

From the botanical point of view, tannins are phenolic substances which give a characteristic appearance in microscopical sections which have been fixed and stained with appropriate reagents. The reagents that have been most commonly employed by plant anatomists are solutions of iron salts such as ferric chloride or ferric acetate. Some investigators have treated the test material with cupric acetate for a week to 10 days followed by immersion for a few minutes in a 5 % solution of ferric acetate. Others have used chromic acid or potassium bichromate for detecting tannins, the reagents giving a bright brown or blackish brown precipitate when tannins are present. A number of other tests have also been used (Haas & Hill, 1921–2; Onslow, 1920).

The present state of knowledge regarding the chemical nature of tannins does not allow of a precise definition of these substances in chemical terms. Buchanan (1952) comes as near as possible to a definition in the following terms: 'the tannins are complex polyhydric phenols having a molecular size and shape which permits suitable solubility in water. They precipitate gelatin and alkaloids from solution, are astringent, give colour reactions with iron salts, form precipitates with many metallic ions, and are rather unstable in the presence of moisture and heat.'

Chemically, leuco-anthocyanins are characterized by the anthocyanidins formed from them when they are digested with mineral acid. With few exceptions these are found to be limited to two only of the seven which, as anthocyanins, occur in petals. These two are cyanidin (I) and delphinidin (II). When isolated from the plant tissues, leuco-anthocyanins show all the properties mentioned above as characteristic of tannins. In considering the relationship between leuco-anthocyanins as tannins on the one hand and as precursors of anthocyanidins on the other, we have also to take into account what is known about the occurrence of tanning materials in plants, and about the chemical properties of such of those materials as have been characterized. There are two especially valuable sources of information under these two headings: *Vegetable Tanning Materials* by F. N. Howes (1953); and *Vegetable Tannins* by E. H. W. Rottsieper (1946).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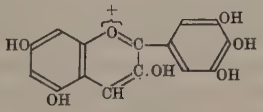
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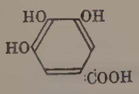
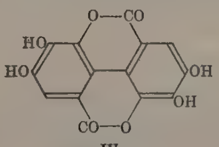
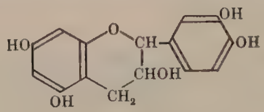
Tannins fall into two groups. The first, known as hydrolysable tannins, usually yield gallic (III) or ellagic acid (IV) and glucose when heated with mineral acid. The second,

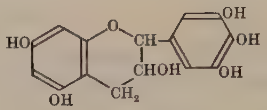

III
Gallic acid


IV
Ellagic acid

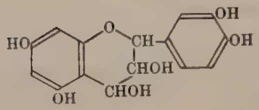
known as condensed tannins, do not yield glucose or other sugars on hydrolysis, but are usually regarded as complex condensation products of substances similar in nature to catechin (V) or gallocatechin (VI). It is currently thought (Bate-Smith & Swain, 1956) that leuco-anthocyanins are usually, in fact, complex substances deriving from simpler molecules possessing the structure VII (in the case of leuco-cyanidin) and VIII (in the



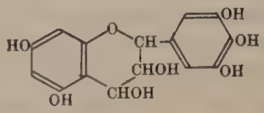
V
Catechin



VI
Gallocatechin



VII



VIII

case of leuco-delphinidin). The close similarity of these structures with those of catechin and gallocatechin is immediately apparent. But the catechins only produce cream to yellowish coloured condensation products when heated with mineral acid—they do not produce the red anthocyanidin characteristic of leuco-anthocyanins when so treated. It is now apparent that leuco-anthocyanins are, in fact, the commonest representatives in Nature of the so-called condensed tannins.

Experimental

I. *Sources of material*

(1) *Anatomical material*

The material used in the present investigation for the microscopical observation of tannins consisted of young twigs, nearly all of which were collected from plants growing at Kew. A few specimens from the Kew museums were also examined, and, as this material is not regarded as satisfactory for the detection of tannins, a note concerning its source has been made in the accompanying tables when the material was obtained from museum specimens. Sometimes additional observations were made on transverse sections of the petioles of leaves from the same species. It is usual to find that when tannins can be detected in stems they can also be detected in petioles from the same species. It should be noted, however, that where tannins occur mainly or exclusively in the bark or superficial tissues of the stem of any particular species they were not invariably detected in petioles. This is no doubt due to the fact that the superficial layers of petioles never consist of bark and are seldom corky.

(2) *Leaf tissues*

Only mature leaves from healthy plants growing under favourable cultural conditions were used. They were as a rule taken immediately into the laboratory for examination. Material sent to the laboratory from a distance was packed in moisture-proof containers and examined if possible within twenty-four hours of picking. With few exceptions, the specimens were taken from, or supplied by, the University Botanic Garden, Cambridge, or the Royal Botanic Gardens, Kew.

II. *Analytical methods*

(1) *Anatomical examination*

It has been our aim, as far as possible, to examine twigs and leaves from the same species both microscopically and by chemical methods. This has not always been possible, however, because of the rather unusual circumstances in which this joint investigation came to be undertaken. The microscopical observations have been made on permanent slides in the reference collection at the Jodrell Laboratory. These slides were not prepared, in the first instance, for the detection of tannins, but for the study of the histology of the plants concerned as a preliminary to writing the reference book entitled *Anatomy of the Dicotyledons* by Metcalfe & Chalk (1950). As is described below, it so happens that the sections were treated in such a way that they at once reveal whether tannins are present in the tissues or not. The slides were made many years before the chemical work on the leaves described in this paper was undertaken. At the time of the chemical investigation it was not always possible to obtain material of precisely the same species as those of which microscope slides were already available. Nevertheless, it has been our aim to base the anatomical and chemical data on closely related, even when it has not been possible to work on precisely the same, species. It will be seen from the accompanying tables that, on the whole, the chemical and anatomical data agree even when closely related rather than identical species have been used.

The cells and tissues that contain tannin can at once be seen in the slides that were examined because they are stained either dark blue to almost black, or exhibit an appreciably darker colour than the non-tanniniferous cells and tissues in the same sections. No such cells occur in sections of species from which tannins are absent, and the proportion of cells that are stained, and the intensity with which they are stained, give a good indication of the quantity of tannin that is present. There are good reasons for believing that whether the cells are stained blue or dark red is correlated with the chemical nature of the tannins.

The fact that tannins are so clearly visible in the slides which were examined during the present investigation is purely accidental, and depends on the technique that was adopted for preparing and staining the sections. It must first be appreciated that the slides in question represent only a relatively small proportion of the many hundreds that are in the slide collection. To prepare these slides with the minimum labour made it necessary to adopt mass production methods, and it was not possible for all of the sections to be treated with the same individual care that would have been possible with smaller numbers of slides. All of the material was first fixed in formalin-acetic-alcohol and it was stored in this reagent until the sections were cut. Sections were cut on a Reichert sledge microtome, after which they were stained in safranin and mounted in canada balsam. Although the material was washed before the sections were cut, it was not entirely free from fixative when it was clamped into the microtome. In consequence the fixative appears to have reacted with the microtome knife to produce an iron salt which then reacted with the tannins in the tissues to give a dark blue or greenish colour depending on the type of tannin that was present. The dark blue of the tanniniferous cells persisted as a counter stain to the safranin in the final preparations, and in species in which the cells were stained green they assumed a dark red colour after being stained with the safranin.

Quite recently a number of tests have been made in order to establish that the staining was due to the causes outlined in the last paragraph. Thus it was found that if sections of fresh material are prepared in exactly the same way, but without the material being fixed in formalin acetic alcohol, the tanniniferous cells are the same colour as, and cannot readily be distinguished from, their neighbours. If a solution of ferric chloride is added to sections of unfixed material the tanniniferous cells are not coloured blue or green. On the other hand, sections of fixed material exhibit the blue or greenish cells if there is sufficient fixative present to act on the microtome knife, and, if the sections are treated with a solution of ferric chloride, the development of the blue or green colour is hastened and intensified. If sections of fixed material showing the blue or green colour are stained in safranin, their final appearance is exactly like that of the slides in the reference collection. The species used for these confirmatory tests were the same as certain of those already in the reference collection of slides, and the new slides showed precisely the same distribution of tanniniferous cells as was to be seen in the reference slides. Tests on non-tanniniferous species also confirmed that none of the cells could be stained dark blue or red by using the same technique.

(2) *Chemical examination*

Full details have been given in earlier papers (Bate-Smith, 1954*a*; Bate-Smith & Lerner, 1954). Essentially the method consists in heating the tissues for 20 min. in aqueous 2 N hydrochloric acid in a test-tube immersed in boiling water, pouring off the aqueous extract, and extracting this with a small volume of ordinary 'amyl' (actually *iso*-amyl) alcohol. The anthocyanidins are concentrated into the supernatant layer, and are identified by paper chromatography (cf. Bate-Smith, 1954*a*). Ellagic acid if present is recognised on the paper chromatogram along with the anthocyanidins (Bate-Smith, 1956*a*) as an unmistakable soft-violet fluorescing spot (R_F in Forestal solvent 0·33 compared with cyanidin 0·50).

For many purposes it may be sufficient to record the mere presence of leuco-anthocyanins, and in relatively what strength. This needs no more than the digestion with mineral acid. Chromatography, which establishes the identity of the anthocyanidins, is an added refinement. The presence of ellagic acid can be demonstrated by a simple test-tube reaction. Some of the leaf tissue is macerated with methyl alcohol, the alcoholic layer (green with dissolved chlorophyll) is poured off, and is treated with a few drops of 5 % acetic acid and a few drops of 5 % sodium nitrite. The solution turns muddy yellow, olive brown, nigger brown, or deep chocolate depending on the amount of ellagic acid present.

RESULTS

The results are given in Table 1. In regard to all data the following symbols are used:

+ + +	very strong positive reaction	±	doubtfully positive or negative
+ +	strong positive reaction	–	negative reaction
+	positive reaction	×	reaction obscured by interfering effect
(+)	weakly positive reaction		

Abbreviations

Authorities for names: usual conventions.

Chemical: L-A = leuco-anthocyanin, L-D = leuco-delphinidin, L-Cy = leuco-cyanidin.

Occurrence of tannins: b. = bark, l. = leaves, f. = fruit, r. = root, loc. = locally, com. = commercial.

ANALYSIS OF RESULTS IN TABLE 1

The number of cases common to the two lists (counting as cases both identical species and species nearly related within the same family) totals 505. Of these, 421, or 83 %, show agreement between the presence or absence of tannin in the stems and the presence or absence of L-A in the leaves. Where agreement is not observed, there are several circumstances which might account for the lack of agreement.

(i) *L-A present in stems but not in leaves.* In several cases this possibility has been tested. In the majority, e.g. *Sambucus nigra*, *Galax aphylla*, *Erythrina crista-galli*, *Passiflora edulis*, *Rhodotypos scandens* and *Urtica dioica*, L-A was, in fact, found to be present in the stems, thus accounting for the discrepancy between the two lists. In a few cases, e.g. *Baptisia australis*, the discrepancy remained. No case was observed in which L-A was present in a stem in which tannin was not recorded. It has not been possible to complete the examination of discrepant species, but it seems clear that many more cases would be explained in this way.

(ii) *Different species examined.* Discrepant cases due to non-identity of species examined would seem likely to occur in such families as Santalaceae, Flacourtiaceae and

TABLE 1

	Anatomical data		Chemical data				
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	Recorded occurrence of useful tannins
Acanthaceae[1]—entirely negative	...	...	...	...	...	...	...
Aceraceae							
Acer campestre Linn	++	In the cork	+	–	+	Ellagic +	In b. of *A. campbellii* Hk. f. and *A. spicatum* Lam.; in l. of *A. ginnala* Max. (gallotannin and ellagic acid)
A. davidi Franch.	...	...	+++	++	+	...	
A. monspessulanum Linn.	...	...	++	+	+	Ellagic +	
A. opulifolium Vill.	++	...	...	...	...	...	
A. platanoides Linn.	++	...	...	...	...	...	
A. pseudo-platanus Linn.	...	...	++	–	+	Ellagic +	
Actinidiaceae							
Actinidia callosa Lindl. (=*kolomikta*)	++	...	+	–	+	...	...
A. chinensis Planch.	...	...	+++	+	++	...	...
Amaranthaceae							
Amaranthus blitum Linn.	–	...	–	–	–	...	In all parts of *Aerva lanata* Juss.
A. hypochondriacus Linn.	–	...	...	...	...	...	
Anacardiaceae							
Cotinus americanus Nutt.	++	...	++	+	+	...	In numerous spp. Some (e.g. quebracho=*Schinopsis* spp.) of major importance (gallo-, ellagi- and condensed tannin)
C. coggygria Scop. *atropurpureus*	...	...	+	+	(+)	...	
Mangifera indica Linn.	++	...	(+)	–	–	...	
Rhus toxicodendron Linn.	+	...	...	...	...	...	
R. trichocarpa Miq.	+	...	...	...	...	...	
Schinus dependens Orteg. var. *ovata*	++	...	...	...	...	...	
S. molle Linn.	...	...	++	+	+	...	
S. terebinthifolius Raddi.	+++	...	...	...	...	...	
Annonaceae							
Asimina triloba Dun.	(+)	Superficial tissue only	++	–	+	...	B. of *Annona muricata* L. and *A. squamosa* L. used loc.
Apocynaceae							
Acokanthera spectabilis Hook. f.	–	...	(+)	–	–	...	B. and r. of *Apocynum venetum* L. said to be used. *Carissa opaca* Stapf.= 'karunda' com.
Allamanda neriifolia Hook.	(+)	Superficial tissue only	–	–	–	...	
Apocynum androsaemifolium Linn.	++	...	++	+	+	...	
Carissa grandiflora A. DC.	+ or ++	...	+	–	++	...	
Gonioma kamassi E. Mey.	–	...	–	–	–	...	
Landolphia kirkii Dyer.	–	...	...	...	...	...	
L. klainii Pierre.	++	...	×	...	...	Purple-blue coloration	
Nerium oleander Linn.	–	...	–	–	–	...	
Strophanthus capensis A. DC.	(+)	Few cells in cortex	...	...	...	...	

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[1] Negative for both tannin and L-A: *Asystasia bella* Benth. & Hook., *Peristrophe speciosa* Nees., *Strobilanthes isophyllus* T. Anders. Negative for tannin: *Beloperone oblongata* Lindl., *Crossandra undulaefolia* Salisb., *Thunbergia natalensis* Hook. Negative for L-A: *Beloperone guttata* T. S. Brandeger, *Crossandra nilotica* Oliver, *Thunbergia alata* B. & J. ex Sims.

Table 1 (*cont.*)

	Anatomical data		Chemical data				
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	Recorded occurrence of useful tannins
Apocynaceae (*cont.*)							
S. divergens R. Grah.	+	Abundant in cork	...	...	...	...	
S. gratus Baill.	...	...	–	–	–	...	
Trachelospermum divaricatum K. Schum.	+	Abundant in cork	...	...	...	...	
T. jasminoides Lem. var. *variegata*	+	In cork and special cells	(+)	–	+	...	
Vinca difformis Poubr.	–	...	...	...	...	...	
V. major Linn.	...	...	–	–	–	...	
V. minor Linn. var. *azurea*	–	...	...	...	...	...	
V. rosea Linn.	...	...	–	–	–	...	
Aquifoliaceae							
Ilex aquifolium Linn.	–	...	–	–	–	...	In b. and l. of *I. paraguariensis* St Hil.; useless for tanning leather
I. paraguariensis St Hil.	+	In superficial tissues only	...	...	...	...	
Araliaceae							
Aralia cachemirica Decne	...	...	(+)	–	–	...	B. of *Horsfieldia sucosa* Warb. used loc.
Fatsia japonica Decne	–	...	–	–	–	...	
Hedera helix Linn.	–	...	–	–	–	...	
Aristolochiaceae							
Aristolochia clematitis Linn.	–	...	–	–	–	...	...
A. sipho L'Hérit.	...	...	–	–	–	...	...
Asarum canadense Linn.	–	...	...	...	...	...	...
A. europaeum Linn.	...	...	–	–	–	...	...
Asclepiadaceae							
Asclepias curassavica Linn.	–	...	–	–	–	...	Gall nuts of *Calotropis gigantea* Ait. said to be used
Periploca graeca Linn.	+	In cork	+	–	+	...	
Vincetoxicum officinale Moench.	–	...	–	–	–	...	
Balsaminaceae							
Impatiens glandulifera Royle	+	...	++	–	+	...	...
Basellaceae							
Boussingaultia baselloides H. B. & K.	–	...	–	–	–	...	...
Begoniaceae							
Begonia corallina Carr.	...	...	+	–	(+)	...	...
B. echinosepala Regel.	+	In cork and phloem only	...	...	...	...	...
B. manicata Cels. ex Vis.	+	Trace in cork	(+)		–	...	...

Berberidaceae							
Berberis darwinii Hook.	+	In cork	(+)	–	+	...	...
Epimedium alpinum Linn.	–	...	...	...	...	...	...
E. perralderianum Coss.	...	...	++	+	+	...	...
E. youngianum Fisch. & Mey.	–	...	...	...	...	...	...
Mahonia aquifolium (Pursh.) Nutt.	+	In superficial tissue only	–	–	–	Senile leaves red not anthocyanin	...
Betulaceae							
Alnus incana Medic.	+	Mainly in young bark	++	–	+	Ellagic +	Alder b. (condensed tannin) used in tanning, but not extensively on account of reddish brown colouring matter
Bignoniaceae							
Campsis radicans Seem.	...	...	–	–	–	...	B. of *Catalpa longissima* Sims. and *Tecoma* spp. used loc.
Catalpa bignonioides Walt.	...	...	–	–	–	...	
Crescentia cujete Linn.	...	...	–	–	–	...	
Incarvillea olgae Regel.	...	...	×	–	–	Green-black L-A reaction	...
I. sinensis Lam.	–	...	...	...	...	...	...
Tecomaria capensis Spach.	...	...	×	...	...	Indigo-blue L-A reaction	...
Bixaceae							
Bixa orellana Linn.	++	...	+	–	+	...	In *Aphloia theaeformis* Benn.
Bombacaceae							
Bombax malabaricum DC.	++	In b. and special cells (mixed with mucilage?)	–	–	–	...	In b. of *Adansonia digitata* L.
Pachira insignis Sauigna	...	...	...	–	–	...	
P. macrocarpa Walp.	++	In special cells in wood and pith and in cork	...	...	...	...	
Boraginaceae[1]							
Anchusa officinalis Linn.	–	Mucilage present?	–	–	–	...	L. of *Halgania lavandulacea* Endl. used loc.
"*Echium fastuosum*"	+	In phloem. Mucilage also?	–	–	–	...	
Lindelofia spectabile Lehm.	+	Mucilage present?	...	...	...	...	
Lithospermum fruticosum Linn. *purpurea-coeruleum*	–	...	–	–	–	...	
Macrotomia echioides Boiss.	+	Mucilage present?	...	...	...	...	
Mertensia echioides Benth.	–	...	...	...	...	...	
Symphytum officinale Linn.	–	Mucilage present	–	–	–	...	
Buxaceae[2]—entirely negative	...	...	...	...	...	...	...
Cactaceae							
Pereskia aculeata Mill.	–	...	...	...	...	...	...
Phyllocactus anguliger Lem	...	...	...	–	–	...	...

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[1] Boraginaceae+records may be due to mucilage.

[2] Negative for both tannin and L-A: *Buxus sempervirens* Linn., *Pachysandra terminalis* Sieb. & Zucc., *Sarcococca humilis* Stapf. Negative for tannin: *Buxus balearica* Lam.

Table 1 (*cont.*)

	Anatomical data		Chemical data				
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	Recorded occurrence of useful tannins
Calycanthaceae							
Calycanthus occidentalis Hook. & Arn.	+	In bark	–	–	–	...	...
Chimonanthus fragrans Lindl.	+	In bark	–	–	–	...	...
Campanulaceae[1]—entirely negative	...	...	...	...	...	...	...
Cannabinaceae							
Cannabis sativa Linn.	–	...	–	–	–	...	...
Humulus lupulus Linn.	(+)	Intense staining in remotely scattered special cells	++	+	+	...	...
Capparidaceae							
Cleome spinosa Jacq.	–	...	–	–	–	...	...
Caprifoliaceae							
Abelia grandiflora Rehd.	(+)	Only very young stem examined	+	...	...	...	...
Dipelta floribunda Maxim.	+	Superficial tissues in young stems	++	...	...	...	...
Lonicera periclymenum Linn.	–	...	–	...	...	...	...
Sambucus ebulus Linn.	+	In a few special cells. More abundant in rhizome than stem	–	...	...	...	...
S. nigra Linn.	+	In bark and special cells	–	–	–	L-A + in stem	...
Viburnum lantana Linn.	...	...	++	–	++	...	...
V. opulus Linn.	++	...	(+)	–	–	...	...
V. tinus Linn.	++	...	...	...	...	...	...
Caricaceae							
Carica papaya Linn.	(+)	In bark only	–	–	–	...	...
Caryophyllaceae[2]—entirely negative		...	...	...	...	...	...
Casuarinaceae							
Casuarina cunninghamiana Miq.	++	...	(+)	–	+	Ellagic +	B. of several spp. of *Casuarina* rich in tannin. (Casuarin=*d*-gallocatechin)
C. stricta Ait.	...	...	+	(+)	+	...	
Celastraceae							
Cassine maurocenia Linn.	++	...	+	+	+	...	*Pterocelastrus variabilis* Sond. and *Elaeodendron* spp. used loc.
Catha edulis Forsk.	+	...	++	++	+	...	
Euonymus europaeus Linn.	–	...	–	–	–	...	
E. latifolius Mill.	+	...	+	–	+	...	

[1] Negative for both tannin and L-A: *Campanula glomerata* Linn., *C. pyramidalis* Linn., *Jasione perennis* Lam., *Platycodon grandiflorum*.

[2] Negative for both tannin and L-A: *Herniaria glabra* Linn., *Silene cucubalus* Wibel., *S. maritima* With. Negative for tannin: *Dianthus campestris* Bieb., *D. giganteus* Uru.=*banaticus* Heuff. ex Griseb., *Lychnis coronaria* Desr., *Stellaria holostea* Linn. Negative for L-A: *Agrostemma githago* L. (*Lychnis githago* (L.) Scop.), *Dianthus alpinus* Linn., *Stellaria media* (L.) Vill.

Cercidiphyllaceae							
Cercidiphyllum japonicum Sieb. & Zucc.	+	In bark	+	–	+	...	...
Chenopodiaceae[1]—entirely negative	...	...	...	...	...	...	...
Chloranthaceae							
Chloranthus afficinalis F. Blume	–	...	...	...	...	...	...
Cistaceae							
Cistus cultivar	...	...	+	+	–	...	*C. salvifolius* L. used loc.
C. incanus Linn. (=*C. polymorphus* Willk.)	++	...	++	...	...	...	...
C. laurifolius Linn.	++	...	...	...	...	...	
Clethraceae							
Clethra alnifolia Linn.	++	...	++	–	++	...	...
C. arborea Ait.	++ or +++	...	+	–	+	...	...
Cneoraceae							
Cneorum tricoccum Linn.	–	...	–	–	–	...	...
Combretaceae							
Combretum erythrophyllum Sond.	–	...	–	–	–	Ellagic +	*Anogeissus latifolia* Wall.= 'dhawa'. *Conocarpus erectus* L.='mangue'. *Laguncularia racemosa* Gaertn.=white mangrove. *Terminalia chebula* Retz.=myrobalans (contains chebulinic acid). Others used loc. (Ellagi- and condensed tannin)
C. grandiflorum G. Don.	...	...	–	–	–	Ellagic ++	
C. platypetalum Welw. ex Laws.	–	...	...	...	...	...	
Terminalia catappa L.	...	...	+	–	+	Ellagic ++	
T. chebula Retz.	+	In cork and special cells	+	...	...	...	
Compositae[2]—all negative except:							
Barnadesia rosea Lindl.	+	In cork only	–	–	–	...	In *Soaresia nitida* Allem.
Cosmos bipinnatus Cav.	...	...	+	–	+	...	
C. diversifolius Otto	(+)	...	...	...	...	...	
Ozothamnus antennaria Hook.	+	Superficial tissue of stem only	–	–	–	...	
Convolvulaceae							
Calystegia sepium R. Br.	–?	Sections of embedded material; staining bluish hue overall	–	–	–	...	...
Convolvulus floridus Linn.	–?		...	...	...	...	...
C. tricolor Linn.	–?		–	–	–	...	...
Ipomoea hederacea Jacq.	–?		...	...	...	...	...
I. purpurea Roth.	–?		–	–	–	...	...
Nolana humifusa (Gouan.) I. M. Johnston	...		–	–	–	...	...
N. tenella Lindl.	–?		...	...	...	...	...

[1] Negative for both tannin and L-A: *Beta maritima* Linn., *Chenopodium bonus-henricus* Linn., *Suaeda fruticosa* Forsk.

[2] Negative for both tannin and L-A: *Arctium lappa* Linn., *Aster novae-angliae* Linn., *Cichorium intybus* Linn., *Echinacea purpurea* Moench., *Eupatorium urticaefolium* Linn., *Inula helenium* Linn., *Olearia albida* Hook. f., *Stifftia chrysantha* Mikan. Negative for tannin: *Arctotis stoechadifolia* Berg., *Centaurea amara* Linn., *Chrysanthemum erubescens* Stapf., *C. morifolium* Ramat., *Coreopsis latifolia* Michx., *Dahlia coronata* Hort. ex Sprague, *D. maximiliana* Hort., *Rudbeckia californica* A. Gray, *Senecio compactus* T. Kirk., *S. grandiflorus* Berg., *S. squalidus* Linn., *Zinnia pauciflora* Linn. Negative for L-A: *Arctotis aspera* Linn., *Centaurea cyanus* Linn., *Chrysanthemum segetum* Linn., *Coreopsis lanceolata* Linn., *Dahlia excelsa*, *D. marckii* Lehm., *D. variabilis*, *Rudbeckia hirta* Linn., *R. speciosa* Wender, *Senecio vulgaris* Linn., *Zinnia angustifolia* H. B. & K.

Table 1 (*cont.*)

	Anatomical data		Chemical data				Recorded occurrence of useful tannins
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	
Cornaceae							
Aucuba japonica Thunb.	–	...	–	–	–	...	*Cornus amomum* Mill.= 'swamp dogwood' used loc. *Curtisia faginea* Ait. used loc. but colour very dark
Cornus macrophylla Wall.	+++	...	(+)	–	(+)	Ellagic +	
C. sanguinea Linn.	++	...	...	...	...	...	
Griselinia littoralis Raoul.	+	Mainly in outer pith	–	–	–	...	
Macrocarpium mas (Linn.) Nakai=*Cornus mas* Linn.	+	...	–	–	–	Ellagic+	
Corylaceae							
Carpinus betulus Linn.	+	Epidermis and cork	–	–	–	Ellagic +; Gallic +	...
Corylus avellana Linn.	+	Especially in cork	+	+	–	...	...
Corynocarpaceae							
Corynocarpus laevigata Forst.	+	Superficial stem tissues	(+)	–	+	Ellagic +	...
Crassulaceae							
Bryophyllum daigremontanum R. Hamet. & Perrier (=*Kalanchoë daigremontanum*)	(+)?	Special cells in cortex (mucilage?)	+?	–	–	...	...
Crassula argentea Thunb. (=*C. portulacea* Lan.)	+	Special cells in ground tissue and phloem	++	++	(+)	...	...
Umbilicus pendulinus D.C. (=*Cotyledon umbilicus*)	+	Special cells in phloem, pith, etc.	...	...	...	...	...
U. rupestris (Salisb.) Dandy	...	...	–	–	–	...	...
Cruciferae[1]—entirely negative	...	...	...	...	...	...	...
Cucurbitaceae							
Bryonia dioica Jacq.	–	...	–	–	–	...	...
Ecballium elaterium A. Rich.	...	...	–	–	–	...	...
Cunoniaceae							
Cunonia capensis Linn.	(++)?	...	++	...	...	...	...
Daphniphyllaceae							
Daphniphyllum macropodium Miq.	+	Cork only	×	–	–	× deep blue → greyish black ppt.	...
Datiscaceae							
Datisca cannabina Linn.	–	...	–	–	–	...	...
Diapensiaceae							
Galax aphylla Linn.	+++	All tissues except wood	–	–	–	L-A ++ in stem; Ellagic +	...

[1] Negative for both tannin and L-A: *Alyssum saxatile* Linn., *Bunias orientale* Linn., *Cheiranthus cheiri* Linn., *Cochlearia lapathifolia* Gilib. (=*C. armoracia* Linn.), *Crambe maritima* Linn., *Iberis sempervirens* Linn., *Isatis tinctoria* Linn., *Lunaria rediviva* Linn.

Dilleniaceae							
Candollea tetrandra Lindl.	++	Especially phloem and pith	+++	++	(+)	...	*Dillenia indica* L. and other spp. used loc.
Hibbertia volubilis Andr.	++	Especially phloem and pith	++	(+)	++	...	
Dipsacaceae[1]—entirely negative	...	...	...	...	...	...	...
Droseraceae							
Drosera binata Labill.	+?	Sections not suitably stained	++	(+)	+	Ellagic (+); some anthocyanin performed	...
D. rotundifolia Linn.	...	...	++	–	+	Ellagic ++; some anthocyanin performed	...
Ebenaceae							
Diospyros kaki Thunb.	++	Not in the wood	+++	++	++	...	Many spp. of *Diospyros* used loc.
D. lotus Linn.	++	All tissues including some ray cells	+	+	+	...	
Elaeagnaceae							
Elaeagnus angustifolia Linn. var. *orientalis*	–	...	–	–	–	...	...
E. multiflora Thunb.	+	Bark and phloem	...	...	...	...	...
E. macrophylla Thunb.	...	...	–	–	–	L-A ++ in stem; Ellagic +	...
E. umbellata Thunb.	+	Cork, phloem and pith	...	...	...	...	...
Hippophaë rhamnoides Linn.	++	Cork and phloem	+	+	+	Ellagic ++	...
H. salicifolia D. Don.	++	Mainly in the cork	+	+	(+)	Ellagic +	...
Elaeocarpaceae							
Aristotelia macqui L'Hérit.	+	Outer cortex and phloem	+	–	+	Ellagic +	In b. of many spp. of *Elaeocarpus*
Tricuspidaria dependens Ruiz. & Pav.	+	Cork, phloem and trace in pith	++	++	+	...	
Ericaceae							
Arbutus andrachne Linn.	++	...	++	+	+	...	L. of *Andromeda polifolia* L.; l., f. and b. of *Arbutus unedo* L.; l. and twigs of *Arctostaphylos uva-ursi* Spreng.; and numerous other spp. used loc. or in the past
A. unedo Linn.	++	...	+++	+	(+)	Ellagic +	
Calluna vulgaris Salisb.	++	...	++	(+)	++	...	
Cassiope tetragona D. Don.	++	In cork and outer pith	++	+	(+)	...	
Daboecia cantabrica K. Koch.	...	...	++	+	+	...	
Erica arborea Linn.	++	...	++	++	–	...	
Erythroxylaceae							
Erythroxylum coca Lam.	...	...	+	–	+	...	L. and b. of *Erythroxylum squamatum* Sw. used loc.
Escalloniaceae							
Anopterus glandulosus Labill.	+	Quite normal as distinct from *Escallonia illinita*	+	–	+	...	...
Carpodetus serratus Forst.	–?	...	(+)	(+)	–	...	...
Escallonia illinita Presl.	+	In phloem (not much in leaf)	×	–	–	× Blue → slate ppt. Amyl pinkish brown	...
E. macrantha Hook. & Arn.	+	...	×	–	–	× Similar	...

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[1] Negative for both tannin and L-A: *Dipsacus fullonum* Linn., *Morina longifolia* Linn., *Scabiosa succisa* Linn. Negative for tannin: *Cephalaria alpina* Schrad., *Scabiosa graminifolia* Linn. var. *rhodopensis*. Negative for L-A: *Cephalaria uralensis* Roem. & Schult. (=*corniculata* Roem. & Schult.).

Table 1 (*cont.*)

	Anatomical data		Chemical data				
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	Recorded occurrence of useful tannins
Escalloniaceae (*cont.*)							
E. montevidensis D.C.	...	...	×	(+)	?	× Slaty ppt. Amyl faintly blue-rose	...
E. rubra Pers.	(+)	Phloem and pith	...	...	...	...	...
Eucommiaceae							
Eucommia ulmoides Oliver	+	Cork only	×	–	+	× Purplish brown cloudy	...
Eucryphiaceae							
Eucryphia glutinosa (Poepp. & Endl.) Baill.	++	...	+	–	+	...	...
Euphorbiaceae							
Acalypha godseffiana Masters	...	...	++	–	+	Ellagic +	B., l. and f. of *Emblica officinalis* Gaertn. much used loc. Many other spp. contain tannin, some used loc.
A. wilkesiana Muell.-Arg. (=*tricolor* Seem.)	–	...	...	...	...	...	
Euphorbia peplus Linn.	–	...	–	–	–	...	
E. spinosa Linn.	–	...	–	–	–	Ellagic +	
Mercurialis perennis Linn.	–	...	–	–	–	...	
Phyllanthus myrtifolius Moon.	+	Chiefly in phloem	...	...	...	...	
P. nivosus Bull.	...	...	–	–	–	...	
Ricinus communis Linn.	–	...	–	–	–	Ellagic +	
Securinega fluggeoides Muell.-Arg.	–	...	–	–	–	...	
Eupomatiaceae							
Eupomatia bennettii F. Muell.	+	Phloem and pith	+++	–	++	...	...
Fagaceae							
Castanea sativa Mill.	+	Mainly in cork	–	–	–	Ellagic ++	Oak, chestnut, valonea, com. tannins (gallo- and ellagitannin)
Fagus sylvatica Linn.	++	...	++	+	+	...	
Nothofagus antarctica Oerst.	++	Mainly outside the wood	...	...	...	...	
N. dombeyi Blume	...	...	–	–	–	Ellagic +	
N. obliqua Blume	++	Mainly outside the wood	...	...	...	...	
Quercus ilex Linn.	++	...	+	–	+	Ellagic +	
Q. suber Linn.	++	...	–	–	–	...	
Ficoidaceae							
Tetragonia expansa Murr.	–	...	–	–	–	...	...
Flacourtiaceae							
Aberia caffra Harv. & Sond.	(+)	Trace in the cork	–	–	–	...	...
Azara dentata Ruiz. & Pav.	–	...	–	–	–	...	...
A. gilliesii Hook. & Arn.	–	...	–	–	–	...	...
Berberidopsis corallina Hook. f.	++	...	++	–	++	...	...
Flacourtia indica Merrill	...	...	–	–	–	...	...
F. prunifolia H. B. & K.	(+)	Trace in the cork and pith	...	...	...	...	...
Hydnocarpus wightiana Blume	+	...	++	...	...	...	...
Kiggelaria africana Linn.	(+)	Strong, but confined to the cork	–	–	–	...	...

Frankeniaceae							
Frankenia laevis Linn.	++	...	–	–	–	Ellagic +	...
Fumariaceae							
Corydalis japonica Mak.	–	...	...	...	...	...	...
C. thalictrifolia Franch.	...	...	–	–	–	...	...
Garryaceae							
Garrya elliptica Dougl. ex Lindl.	–	...	×	–	–	× Dk. brown	...
Gentianaceae[1]—entirely negative	...	...	...	...	...	...	...
Geraniaceae							
Geranium phaeum Linn.	(+)?	...	–	–	–	Ellagic +	R. of several spp. of *Geranium* rich in tannin
G. pyrenaicum Burm.	...	...	–	–	–	Ellagic +	
G. robertianum Linn.	–	...	...	...	...	...	
Pelargonium zonale L'Hérit. ex Soland.	–	...	–	–	–	...	
Gesneriaceae[2]—entirely negative	...	...	...	...	...	...	...
Grossulariaceae							
Ribes aureum Pursh.	++	Cork, phloem and pith	+	–	–	Ellagic ++	...
R. grossularia Linn.	++	Particularly in cork	++	+	(+)	...	...
R. nigrum Linn.	++	...	++	+	(+)	...	...
R. sanguineum Pursh.	++	...	+++	++	(+)	...	...
Guttiferae							
Clusia flava Jacq.	...	...	++	–	++	...	F. of *Garcinia mangostana* L. (mangosteen) used loc. Other spp. contain tannin
Clusia sp.	++	...	...	...	...	...	
Haloragidaceae							
Haloragis alata Jacq.	(+)	In phloem	+	–	+	Ellagic +	R. of *Gunnera chilensis* Lam. used loc.
Hamamelidaceae							
Corylopsis spicata Sieb. & Zucc.	+++	...	+++	++	(+)	...	B. of *Hamamelis virginiana* L. (witch hazel) contains a crystallizable gallo-tannin
Hamamelis japonica Sieb. & Zucc. var. *arborea*	++	...	...	...	...	...	
H. mollis Oliver ex Forb. & Hemsl.	++	...	+	+	+	...	
Liquidambar formosana Hance	++	...	×	–	–	× Br. blue-green becoming brown. Ellagic +	
Sinowilsonia henryi Hemsl.	–	...	–	–	–	...	
Sycopsis sinensis Oliver	++	...	+	+	(+)?	...	
Hippuridaceae							
Hippuris vulgaris Linn.	–	...	–	–	–	...	...

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[1] Negative for both tannin and L-A: *Gentiana septemfida* Pall., *Menyanthes trifoliata* Linn. Negative for tannin: *Gentiana asclepiadea* Linn.

[2] Negative for both tannin and L-A: *Columnea gloriosa* Sprague, *Streptocarpus caulescens* Vatke. Negative for tannin: *Streptocarpus holstii* Engl., *S. johannis* L. L. Britten. Negative for L-A: *S. rexii* Lindl.

Table 1 (*cont.*)

	Anatomical data		Chemical data				
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	Recorded occurrence of useful tannins
Hydrangeaceae							
Deutzia setchuenensis Franch.	+	Mostly in cork, trace in phloem	–	–	–	...	...
Dichroa febrifuga Lour.	(+)	Intense in hypodermis, also in petiole	+++	++	(+)	...	...
Philadelphus lewisii Pursh.	+	Cork only	+	–	+	...	...
Hydrophyllaceae							
Hydrophyllum canadense Linn.	...	...	–	–	–	...	...
H. virginicum Linn.	–	...	...	...	...	...	...
Phacelia tanacetifolium Benth.	–	...	–	–	–	...	...
Hypericaceae							
Hypericum androsaemum Linn.	+	...	...	...	...	...	...
H. calycinum Linn.	...	...	+++	(+)	++	...	...
H. lanceolatum Lam.	++	...	...	...	...	...	...
Juglandaceae							
Juglans regia Linn.	+?	Staining faint	+++	–	+	...	Nutshells of *Carya illinoensis* Koch. (pecan), b. of *Engelhardtia spicata* Blume, f. of *Juglans regia* L., f. of *Platycarya strobilacea* Sieb. & Zucc. used loc.
Labiatae[1]—entirely negative	...	...	...	...	...	...	...
Lardizabalaceae							
Akebia lobata Decne	+	Abundant in cork	–	–	–	...	...
A. quinata D.C.	+	In cork	×	–	–	× Dk. brown	...
Holboellia coriacea Diels	+	In parts of epidermis and lenticels	...	...	...	...	...
H. latifolia Wall.	...	...	(+)	–	+	...	...

[1] Negative for both tannin and L-A: *Ballota nigra* Linn., *Elsholtzia stauntoni* Benth., *Glechoma hederacea* Linn., *Horminum pyrenaicum* Linn., *Hyssopus officinalis* Linn., *Lamium album* Linn., *Lycopus europaeus* Linn., *Nepeta mussini* Spreng ex Henck., *Prostanthera sieberi* Benth., *Stachys officinalis* (L.) Trevis. Negative for tannin: *Prostanthera melissifolia* F. Muell., *Scutellaria lateriflora* Linn., *Stachys germanica* Linn., *S. sylvatica* Linn. Negative for L-A: *Phlomis fruticosa* Linn., *Scutellaria peregrina* Linn.

Lauraceae							
Cinnamomum camphora Nees & Eberm.	+	Mainly in phloem	+	–	+	...	*Laurus peumo* Domb. (=*Cryptocarya peumis*) used loc. B. of *Persea lingua* Nees and *P. meyeniana* Nees (Persea or Valdivia bark) once used extensively for tanning Valdivia leather
C. zeylanicum Nees	++	...	...	...	...	...	
Laurus nobilis Linn.	++	...	+	–	(+)	...	
Lindera benzoin Meissn.	+	In cork	+	–	+	...	
Persea gratissima Gaertn.	++	...	...	...	...	...	
P. lingua Nees	...	...	+	–	+	...	
Umbellularia californica Nutt.	++	Heavy in but not confined to cork	(+)	...	(+)?	...	
Leguminosae							
Mimosaceae:							
Acacia armata R. Br.	+++	...	++	++	(+)	...	Wattle, cutch, sant, com. tannins; other spp. used loc.
A. decurrens Willd. var. *dealbata*	+	...	+	–	(+)	...	
Pithecolobium dulce Benth.	+	Cork and phloem	+	...	(+)	...	
Caesalpiniaceae:							
Bauhinia forficata Link	(+)?	Staining not typical	...	...	...	...	Avaram, divi-divi, algarobilla (contains brevifolin), tara, teri, sant, com. tannins. (Ellagi- and condensed tannins)
B. yunnanensis Franch.	...	...	+	–	+	...	
Caesalpinia japonica Sieb. & Zucc.	++	...	+	–	+	...	
Cassia corymbosa Lam.	...	...	–	–	–	...	
C. grandis Linn.	+	...	...	...	...	...	
Cercis siliquastrum Linn.	++	...	+++	++	+	...	
Saraca cauliflora Baker	...	...	++	++	(+)	...	
S. declinata Miq.	++	...	...	...	...	...	
Papilionaceae:							
Abrus precatorius Linn.	+	In cork	...	...	...	...	Numerous spp. contain tannin but none of com. importance
Amicia zygomeris DC.	...	...	(+)	–	–	...	
Arachis hypogaea Linn.	(+)	In pith	(+)	–	–	L-A ++ in testa	
Baptisia australis R. Br.	(+)	Trace near lenticels	–	–	–	L-A – in stems	
Derris elliptica Benth.	...	...	++	–	+	...	
D. malaccensis Prain	+	...	...	...	...	...	
Erythrina crista-galli Linn.	+	In numerous isolated cells i cortex and phloem	–	–	–	L-A + in stem	
Galega officinalis Linn.	–	...	–	–	–	...	
Lathyrus luteus Munby	...	...	–	–	–	...	
L. maritimus Bigel.	–	...	...	...	...	...	
L. pratensis Linn.	(+)	In the epidermis	...	...	...	...	
L. sylvestris Linn.	–	...	...	...	...	...	
L. venetus Rouy	...	...	–	–	–	...	
Petteria ramentacea Prsl.	+	In outer cortex	–	–	–	...	
Phaseolus multiflorus Willd.	–	...	...	...	...	...	
P. vulgaris Linn.	...	...	–	–	–	L-A ++ in testa	
Psoralea macrostachys DC.	(+)	Trace in special cells	–	–	–	...	
Rhynchosia phaseoloides DC.	...	...	++	++	(+)	...	
Robinia pseudacacia Linn.	+	In cork and special cells	++	++	+	...	
Sophora japonica Linn.	–	Very young stem	–	–	–	...	
Spartium junceum Linn.	–	...	–	–	–	...	

Table 1 (*cont.*)

	Anatomical data		Chemical data				Recorded occurrence of useful tannins
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	
Leguminosae (*cont.*)							
Thermopsis montana Nutt. ex Torr. & Gray	(+)	Trace in a few epidermal cells	(+)	–	–	...	
Vicia cracca Linn.	–	...	...	...	...	...	
V. faba Linn.	...	...	–	–	–	L-A ++ in testa	
V. gigantea Hook.	–	...	...	...	...	...	
Wistaria chinensis DC.	+	In cork and special cells	++	–	+	...	
Lentibulariaceae							
Utricularia caerulea Linn.	...	...	–	–	–	...	...
U. minor Linn.	–	...	...	...	...	...	...
Limnanthaceae							
Limnanthes douglasii R. Br.	...	...	++	+	+	...	...
Linaceae							
Linum perenne Linn.	–	...	–	–	–	...	...
Reinwardtia tetragyna Planch.	(–)	Trace in the cork?	–	–	–	...	...
Loasaceae							
Blumenbachia hieronymii Urb.	–	...	...	...	...	...	...
B. insignis Schrad.	...	...	–	–	–	...	...
Loasa vulcanica André	–	...	...	...	...	...	...
Mentzelia lindleyii Torr. & Gray	...	...	–	–	–	...	...
Lobeliaceae							
Centropogon lucyanus Schoenland	–	...	(+)	–	(+)	Ellagic +	...
Lobelia gibberoa Hemsl.	...	...	–	–	–	...	...
Loganiaceae							
Buddleja asiatica Lour.	...	...	–*	–	–	*Deep golden-brown	...
B. colvilei Hook. f. & Th.	(–)?	Trace in epidermis?	...	...	...	...	...
B. globosa Hope	–	...	...	...	...	...	...
B. paniculata Wall.	(–)?	Trace in epidermis?	...	...	...	...	...
Desfontainea spinosa Ruiz. & Pav.	(–)?	Trace in epidermis?	–	–	–	...	...
Nicodemia diversifolia Tenore	+	In epidermis	–	–	–	...	...
Loranthaceae							
Arceuthobium oxycedri Linn.	+	...	++	++	(+)	...	Many rich in tannin. *Nuytsia floribunda* L-A and ellagic +
Viscum album Linn.	–	...	–	–	–	...	
Lythraceae							
Lagerstroemia indica Linn.	(+)	In the cork	–	–	–	Ellagic +	*Lagerstroemia parviflora* Roxb. used loc.; l. of *Lawsonia alba* Lam. (henna) used for tanning as well as dyeing; *Pemphis acidula* Forst. used loc.
Lythrum salicaria Linn.	(+)	In the cork	–	–	–	Ellagic ++	

Magnoliaceae							
Liriodendron tulipifera Linn.	+	In the cork	×	–	(+)?	× Imm. bl.-mauve fading to cloudy brown-yellow	...
Magnolia grandiflora Linn.	–	No cork in sections	+	...	...	...	...
M. virginiana Linn.	+	In the cork	(+)	...	...	...	...
Michelia excelsa Blume	(+)	Trace in the cork	...	...	...	...	...
M. fuscata Blume	...	...	+	–	–?	Bl.-pink, fading, cloudy	...
Malpighiaceae							
Heteropteris chrysophylla H. B. & K.	–	...	...	...	...	...	B. of *Byrsonima spicata* Rich. and other spp. of *Byrsonima* used
H. umbellata A. Juss.	...	...	–	–	–	...	
Hiptage madablota Gaertn.	++	...	++	–	++	...	
Malpighia coccigera Linn.	...	...	++*	–	–	*Leuco-pelargonidin	
M. nitida Cranz.	+	Only in the cork	...	...	...	...	
Malvaceae							
Abutilon insigne Planch.	(+)?	Special cells in the pith ? Mucilage	–	–	–	...	...
Althaea rosea Cav.	(+)?	Special cells in cortex and pith	–	–	–	...	...
Gossypium herbaceum Linn.	...	...	++	+	+	...	...
Gossypium sp.	+	Special cells mainly phloem and pith	...	...	...	...	...
Hoheria sexstylosa Colenso	+	Mainly in the cork	(+)	–	+	...	...
Lagunaria patersonii G. Don.	+	Cork and special cells	–	–	–	...	...
Pavonia rosea Schlect.	–	...	++	–	+	...	...
Sphaeralcea fendleri A. Gray	–	...	...	...	...	...	...
S. umbellata G. Don	...	...	–	–	–	...	...
Melastomaceae							
Medinilla magnifica Lindl. var. *superba*	+	Mainly in outer pith	++	++	(+)	Ellagic +	...
Tibouchina semidecandra Cogn.	+	...	+++	+	+	Ellagic +	...
Meliaceae							
Melia azedarach Linn.	+	Only in the cork	–	–	–	...	*Carapa guianensis* Aubl. and b. of *Cedrela toona* Roxb. used loc. B. of *Khaya senegalensis* A. Juss. sometimes so used. B. of *Soymida febrifuga* Juss. yields light-coloured leather
Swietenia mahagoni Jacq.	+++	...	++	...	...	...	
Melianthaceae							
Greyia sutherlandii Hook. & Harv.	...	...	–	–	–	Ellagic ++	...
Melianthus major Linn.	–	...	...	...	...	...	...
Melianthus sp.	...	...	–	–	–	Ellagic ++	...
Menispermaceae							
Cocculus laurifolius DC.	...	...	–	–	–	...	...
C. trilobus DC.	+?	In cork?	...	...	...	...	...
Stephania rotunda Lour.	–	...	–	–	–	...	...

Table 1 (*cont.*)

	Anatomical data		Chemical data				
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	Recorded occurrence of useful tannins
Monimiaceae							
Doryphora sassafras Endl.	+	Mainly cork and phloem	+	−	+	...	...
Laurelia nova-zelandiae A. Cunn.	+	Cork and phloem	+	−	−	...	...
Peumus boldus Molina	+	Mainly in pith	−	−	−	...	...
Moraceae							
Ficus carica Linn.	+	In cork only	−	−	−	...	B. of *Artocarpus* spp. used loc. *Cecropia* spp., *Ficus* spp., *Maclura aurantiaca* Nutt. (=*M. pomifera*) used loc.
F. elastica Roxb.	++	...	+	−	+	...	
Morus nigra Linn.	+	In cork only	−	−	−	...	
Moringaceae							
Moringa oleifera Lam.	...	...	−	−	−	...	...
Myoporaceae							
Myoporum laetum Forst.	(+)?	Trace in epidermis	−	−	−	...	...
M. serratum R. Br.	+	Epidermis and cork	−	−	−	...	...
Myricaceae							
Myrica gale Linn.	+++	Cork, phloem and pith	++	+	(+)	...	*Myrica gale* L. and *M. nagi* Thb. have been used
Myrsinaceae							
Ardisia crispa A. DC.	++	...	++	+	+	...	*Ardisia serrata* Pers. furnishes a good tan bark
Myrsine africana Linn.	+++	...	+	+	−	...	
Myrtaceae							
Agonis flexuosa Lindl.	+	Mainly cork and phloem	++	+	+	Ellagic (+)	Kino and b. of many spp. rich in tannin (mixed). Mallett= *Eucalyptus astringens*. B. and l. of *Psidium guajava* L. (guava) used loc. Also b. of *Syzygium* spp. and *Tristania conferta* Griff.
Angophora cordifolia Cav.	++	Epidermis, phloem and pith	+	−	+	...	
Callistemon citrinus Stapf.	++	Cork, phloem and pith	(+)	?	?	Ellagic +	
Calothamnus lateralis Lindl.	++	Phloem and pith	...	...	...	...	
C. rupestris Schau.	...	...	++	(+)	+	...	
Eucalyptus calophylla R. Br.	+++	...	++	+	+	Ellagic +	
E. ficifolia F. Muell.	+++	Cortex, phloem and pith	++	+	+	Ellagic +	
Eugenia chequen Molina	++	Chiefly phloem and pith	(+)	?	?	...	
Feijoa sellowiana Berg.	+	...	+	−	+	Ellagic ++	
Melaleuca styphelioides Sm.	+?	Staining not typical	++	++	+	Ellagic +	
Myrtus communis Linn. var. *tarentina*	+++	Cortex, phloem and pith	(+)	?	−	Ellagic +	
Psidium cattleianum Sabine	+++	Cortex, phloem and pith	++	−	+	Ellagic ++	
Nepenthaceae							
Nepenthes distillatoria Linn.	...	...	+	−	+	...	.
N. ratcliffiana hort. cult. var.	++	Epidermis, cortex, phloem, rays	...	...	...	...	.

Nyctaginaceae							
Bougainvillea glabra Choisy	(+)	Trace in cork	–	–	–	...	...
Mirabilis jalapa Linn.	–	...	–	–	–	...	...
Oxybaphus nyctagineus Sweet	–	...	...	...	...	...	...
Nymphaeaceae							
Nuphar luteum Sibth. & Sm.	–	...	–	–	–	Ellagic +	Rhizomes of *Nymphaea alba* L. said to be used loc.
Nymphaea gigantea Hook. var. *alba*	–	...	...	...	...	...	
Nymphaea var. *Harrastick*	...	...	...	–	(+)	...	
Nymphaea lotus Linn.	–	...	...	...	...	...	
Victoria amazonica Sowerby	...	...	...	...	...	Rhizome L-A +	
Nyssaceae							
Davidia involucrata Baill. var. *vilmoriniana* (Dode.) Wang.	+	Bark only	–	–	–	Ellagic +	...
Oleaceae							
Chionanthus retusa Lindl.	–	...	–	–	–	...	B. of *Nyctanthes arbortristis* L. said to have been used
Fontanesia phillyreoides Labill.	(+)	Trace in the epidermis	–	–	–	...	
Fraxinus excelsior Linn.	–	...	–	–	–	...	
Jasminum humile Linn.	–	...	...	–	...	...	
J. primulinum Hemsl. ex Baker	...	...	–	–	–	...	
J. pubigerum D. Don	(+)	Trace in cork, etc.	...	...	...	...	
Ligustrum vulgare Linn.	(+)	Trace in cork	–	–	–	...	
Olea europaea Linn.	(+)	Trace in cork	–	–	–	...	
Phillyrea decora Boiss. & Bal.	–	...	–	–	–	...	
Onagraceae							
Fuchsia bacillaris Lindl.	...	...	–	–	–	Ellagic +	...
F. corymbiflora Ruiz. & Pav.	...	...	–	–	–	Ellagic +	...
F. magellanica Lam. (=*macrostemma* Ruiz. & Pav.)	+	In the phloem	...	...	...	...	...
F. pumila Hort. ex Meunissier	...	...	...	...	...	...	...
Oenothera hirsuta Steud.	...	...	–	–	–	Ellagic +	...
O. purpurea Curt.	+	...	...	...	...	...	...
Orobanchaceae							
Lathraea clandestina Linn.	...	...	×	–	–	× Purplish brown	...
L. squamaria Linn.	–?	Staining not typical	...	...	...	...	...
Oxalidaceae							
Averrhoa carambola Linn.	++	...	++	–	+	...	B. of *Oxalis gigantea* Barn. much used loc.
Oxalis bupleurifolia St. Hil.	...	...	++	+	(+)	...	
Papaveraceae[1]—entirely negative	...	...	...	...	...	...	...
Passifloraceae							
Passiflora capsularis Linn.	...	...	–	–	–	...	*Adenia* tanniniferous
P. edulis Sims	...	...	–	–	–	L-A (+) in stem	
P. quadrangularis Linn.	+	Only in cork	...	...	...	...	
P. racemosa Brot.	+	Only in cork	...	...	...	...	

[1] Negative for both tannin and L-A: *Chelidonium majus* Linn. Negative for tannin: *Macleaya microcarpa* Fedde, *Romneya trichocalyx* Eastw. Negative for L-A: *Glaucium flavum* Crantz., *Meconopsis cambrica* Vig., *Papaver orientale* Linn.

Table 1 (*cont.*)

	Anatomical data		Chemical data				Recorded occurrence of useful tannins
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	
Phytolaccaceae							
Phytolacca acinosa Roxb.	–	...	...	...	...	...	...
P. clavigera W. W. Smith	...	...	–	–	–	...	...
Piperaceae							
Peperomia langsdorfii Miq.	–	...	...	...	...	...	...
P. tithymaloides A. Dietr.	...	...	–	–	–	...	...
Piper excelsum Forst. (=*Macropiper excelsum* Miq.)	–	...	–	–	–	...	...
Pittosporaceae							
Pittosporum dallii Cheeseman	+	In the cork only	–	–	–	...	...
P. eugenioides A. Cunn.	–	No cork on section	–	–	–	...	...
P. patulum Hook. f.	+	In the cork only	–	–	–	...	...
P. tenuifolium Bank. & Soland.	+	In the cork only	–	–	–	...	...
P. undulatum Vent.	...	...	(+)	–	(+)?	...	...
Sollya heterophylla Lindl.	+	In the cork only	–	–	–	...	...
Plantaginaceae							
Plantago cynops Linn.	–	...	–	–	–	...	...
Plumbaginaceae							
Armeria lusitanica Link (=*pinfolia* Hoffmgg. & Link)	...	...	++	++	–	...	*Limonium vulgare* Mill. (=*Statice limonium*), Sea Lavender, and *L. gmelinii* Willd. and *L. latifolia* Sm. 'kermek' used com. *Plumbago europaea* L. used loc.
A. maritima Willd.	+++	All tissues	++	++	–	...	
Limonium latifolium Moench.	+++	All tissues	++	+	–	...	
Plumbago europaea Linn.	++	All tissues	++	+	+	...	
Polemoniaceae							
Cobaea scandens Cav.	(+)	Mainly in phloem	+?*	–	(+)?	*Purplish pink	...
Polemonium caeruleum Linn.	–	...	–	–	–	...	...
Polygalaceae							
Polygala chamaebuxus Linn. var. *grandiflora*	–		–	–	–	...	...
Polygonaceae							
Fagopyrum cymosum Meissn.	+?	Mainly in phloem, not well stained	...	...	...	...	*Polygonum alpinum* All., 'taran', used com., other spp. used loc. *P. bistorta* L. contains ellagic acid. *Rheum* spp. (Turkmen-Rhubarb) suitable for tanning. Canaigre=*Rumex hymenosepalus* Torr. Other *Rumex* spp. contain similar tannin. (Condensed)
F. tataricum Gaertn.	...	...	++	(+)	+	...	
Polygonum alpinum All.	...	...	+	...	...	...	
P. aubertii	...	...	+	...	...	...	
P. aviculare Linn.	...	...	+	+	+	...	
P. bistorta Linn.	+?	Mainly in phloem, not well stained	...	...	...	...	
P. cuspidatum Sieb. & Zucc.	+	Cortex and phloem, not well stained	...	...	...	...	

Polygonaceae (*cont.*)							
P. equisetiforme Sibth. & Sm.	++	Cortex, phloem and outer part of pith	...	...	...	...	
P. hydropiper Linn.	...	...	++	...	...	...	
P. persicaria Linn.	...	...	+	...	...	...	
Rumex acetosa Linn.	+	Mainly in phloem, not well stained	++	(+)	+	...	
Portulacaceae							
Portulaca grandiflora Hook.	–	...	–	–	–	*Portulacaria afra* leaves L-A+(L-Cy)	...
P. oleracea Linn.	–	...	–	–	–	...	...
Primulaceae							
Anagallis arvensis Linn.	(+)	A few cells in phloem	...	...	...	...	...
Cyclamen persicum Mill.	...	...	+++	+	(+)	...	...
Lysimachia vulgaris Linn.	++	Cortex and pith	++	++	(+)	...	...
Primula veris Linn.	+	Scattered cells in peduncle	+++	++	(+)	...	...
P. vulgaris Huds.	++	Scattered cells in leaf base	+++	+	(+)	...	...
Soldanella alpina Linn.	...	...	–	–	–	...	...
Proteaceae							
Banksia integrifolia Linn.	+++	Cork, phloem and pith	++	+	(+)	...	Many spp. rich in tannin. B. of *Protea* spp. once used loc.
B. serrata L. f.	+++	Cork, cortex, phloem, rays and pith	...	...	...	...	
Grevillea robusta A. Cunn.	++	Cork, cortex, phloem, rays and pith	++	+	–	...	
Hakea scoparia Meiss.	++	Cork, cortex, phloem, rays and pith	+	+	(+)	...	
Lomatia silaifolia R. Br.	+++	Cork, cortex, phloem, rays and pith	+++	+	(+)	...	
Macadamia ternifolia F. Muell.	++	Cork, cortex, phloem, rays and pith	++	+	+	...	
Protea cynaroides Linn.	+	Chiefly cork and ray cells	++	?	?	Brown trail overall	
Stenocarpus sinuatus Endl.	...	Chiefly cork and cortex	+	–	+	...	
Punicaceae							
Punica granatum Linn.	–	...	–	–	–	Ellagic ++	B. and f. shells of *P. granatum* L. once used extensively in tanning. (Ellagitannin)
Ranunculaceae							
Adonis vernalis Linn.	–	...	...	...	...	...	...
A. vulgaris	...	...	–	–	–	...	...
Clematis afoliata J. Buch.	–	...	...	...	...	...	...
C. heracleaefolia DC.	...	...	–	–	–	...	...
C. vitalba Linn.	(+)	In b. Staining not very pronounced	...	...	...	...	...
Myosurus minimus Linn.	–	...	–	–	–	...	...

Table 1 (*cont.*)

	Anatomical data		Chemical data				Recorded occurrence of useful tannins
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	
Ranunculaceae (*cont.*)							
Paeonia arietina Anders. (=*peregrina* Mill?)	...	...	–	–	–	...	...
P. sp.	–	...	...	...	...	...	...
Ranunculus acris Linn.	–	...	–	–	–	...	...
Thalictrum glaucum Desf.	–	...	–	–	–	...	...
Trollius europaeus Linn.	–	...	–	–	–	...	...
Zanthorhiza apiifolia L'Hérit.	–	...	–	–	–	...	...
Resedaceae							
Reseda odorata Linn.	–	...	–	–	–	...	...
Rhamnaceae							
Colletia armata Miers (=*spinosa* Lam.)	–	...	–	–	–	...	Numerous spp. contain tannin. *Zizyphus* spp. used loc.
Frangula alnus Mill. (=*Rhamnus frangula* Linn.)	+	Cork	(+)	–	(+)?	...	
Pomaderris apetala Labill.	++	Cork, phloem and pith	...	–	+	...	
Rhamnus cathartica Linn.	+	Cork and phloem	+	+	(+)	...	
R. purshiana DC.	...	...	+	+	+	...	
Rhizophoraceae							
Bruguiera gymnorhiza Lam.	++	Mainly in b.	...	...	...	...	Mangrove largely provided by this family, especially *Bruguiera* spp., *Ceriops* spp. and *Rhizophora* spp. Constitution uncertain
Cassipourea verticillata N. E. Br.	...	...	+	–	–	Leuco-pelargonidin! Ellagic (+)	
Rosaceae							
Agrimonia eupatoria Linn.	++	Cortex, phloem and pith	++	–	++	...	Many spp. rich in tannin. F. of *Chrysobalanus icaco* L. used. R. of *Potentilla tormentilla* Neck. etc. used loc. at one time. B. of *Sorbus aucuparia* L. and *S. domestica* L. said to tan well. L. of *Filipendula ulmaria* Max. used loc. Ellagic acid present only in the tribe Rosoideae. Catechins often present
Amelanchier canadensis Medic.	++	Cork, rays and pith	...	...	...	...	
A. florida Lindl.	...	...	++	–	+	...	
Crataegus carrieri Vauvel.	+	Cork only	...	...	...	...	
C. crus-galli Linn.	...	...	...	...	...	...	
C. monogyna Jacq.	++	Cork, cortex, phloem, rays, pith	... ...	...	...	...	
C. pyracantha Medic.	...	...	+++	–	++	...	
Eriobotrya japonica Lindl.	+	Chiefly phloem and pith	+++	–	++	...	
Filipendula ulmaria (L.) Maxim.	(+)	Near epidermis	++	...	...	...	
Fragaria indica Andr.	(+)	Trace in cortex?	...	...	...	...	
F. moschata Duchesne	...	...	+	...	+	...	
Fragaria (Strawberry) 'Auchincruive Climax', etc.	...	...	+	–	+	Ellagic +	
Geum urbanum Linn.	(+)	Trace in epidermis	–	–	–	Ellagic +	
Kerria japonica DC.	+	Conspicuous in endodermis	+	–	+	...	
Malus floribunda Sieb.	+	Cork only	...	...	...	...	

Rosaceae (*cont.*)							
M. pumila Mill.	+	Cork only	...	...	...	...	
M. sargenti Rehd.	...	...	+	−	+	...	
Neillia longiracemosa Hemsl.	...	...	++	−	++	...	
N. sinensis Oliver	++	Cork, phloem, outer pith	...	...	...	...	
Photinia serrulata Lindl.	++	Especially cork and phloem	++	−	++	...	
Potentilla fruticosa Linn.	++	Cork, phloem, outer pith	++	−	+	...	
P. rupestris Linn.	...	...	−	−	−	Ellagic +	
Prunus cerasifera Ehrh. var. *pissardii* Carr.	(+)	Stem very young; trace under epidermis	++	−	++	...	
P. laurocerasus Linn.	++	Cork, cortex, phloem, pith	++	−	++	...	
Raphiolepis umbellata Mak.	++	Cork, phloem and pith	++	−	+	...	
Rhodotypos scandens Mak.	+	In cork staining not pronounced, but present in many ray cells	−	−	−	L-A + in stem	
Rosa bracteata Wendl.	...	...	−	−	−	Ellagic +	
R. canina L. Agg. var.	+	Chiefly cork and pith	...	...	...	...	
R. hugonis Hemsl.	+	Abundant in cork	...	...	...	...	
R. multiflora Thunb.	...	...	++	...	...	...	
R. soulieana Crep.	...	...	(+)	...	...	...	
Rosa sp. 'Dorothy Perkins'	+	Cork and phloem	...	...	...	...	
Rubus deliciosus Torr.	+	Abundant in cork	−	−	−	Ellagic +	
Sorbus aucuparia Linn.	...	...	++	−	+	...	
Spiraea bracteata Rafin.	+	Abundant in cork	...	...	...	...	
S. salicifolia Linn.	...	...	++	−	++	...	
Rubiaceae							
Cinchona succirubra Pav. ex Klotzsch	+	Chiefly in cork	−	−	−	...	Gambier=*Uncaria gambir* Roxb. (condensed). B. of *Oldenlandia umbellata* L. used loc.
Coffea arabica Linn.	(+)	A few cells in the phloem	+	−	+	...	
Galium verum Linn.	(+)	Trace in the cork	×	...	...	× Purplish brown	
Ixora kewensis Hort.	+++	...	+++*	−	+	*Crimson purplish; brown-pink trail	
I. oculata Hort.	+++	Cork, cortex, phloem, rays, pith	...	...	...	...	
Luculia gratissima Sweet	+	Scattered cells	+	−	+	...	
Manettia inflata Sprague	−	...	−*	−	−	*Brownish	
Mitriostigma axillare Hochst.	+	Scattered cells in phloem and cortex	+	−	++	...	
Rondeletia cordata Benth.	++	Abundant in cork, cortex and phloem	++	+	+	...	
Rutaceae							
Boronia heterophylla F. Muell.	...	...	+	+	−	...	...
Choisya ternata H. B. & K.	−	...	−	−	−	...	...
Citrus aurantium Linn.	−	...	−	−	−	...	...
Coleonema album Bartl. & Wendl.	+	In cork	+	(+)	(+)?	...	...
Correa speciosa Ait.	(+)	Below epidermis. Stem very young	+++	++	++	...	...

Table 1 (*cont.*)

	Anatomical data		Chemical data				Recorded occurrence of useful tannins
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	
Rutaceae (*cont.*)							
Crowea saligna Andr.	+	Below epidermis and in pith. Stem very young	+++	++	(+)	...	
Eriostemon myoporoides DC.	(+)	In cortex	(+)	–	–	...	...
Evodia micrococca F. Muell.	+	In cork and inner cortex	++	+	(+)	...	...
Murraya exotica Linn.	–	...	–	–	–	...	...
Poncirus trifoliata Raf.	–	...	–	–	–	...	...
Ptelea trifoliata Linn.	+	Abundant in cork	–	–	–	...	...
Skimmia japonica Thunb.	–	...	–	–	–	...	...
Zanthoxylum alatum Roxb.	...	...	++	–	+	...	...
Z. americanum Mill.	+	In cork	–	...	...	...	...
Z. bungei Planch.	+	In cork	++	...	...	...	...
Sabiaceae							
Meliosma beaniana Rehder & Wilson	+	Cork and outer pith	...	...	...	...	...
M. cuneifolia Franch.	++	Cork, ray cells and outer pith	...	...	...	...	...
M. oldhamii Miq.	...	...	+	–	+	...	...
Salicaceae							
Populus alba Linn.	+	Cork and cortex	...	...	...	...	B. of *Populus pyramidalis* Salisb. and *P. tremula* L. have been used loc. B. of several spp. of *Salix* (willow) used com. (condensed)
P. canescens Sm.	...	...	++	–	+	...	
P. tremula Linn.	+	In cork	–	–	–	...	
P. trichocarpa Torr. & Gray	(+)	Trace in cork	...	...	...	...	
Salix acutifolia Willd.	...	...	+	...	...	...	
S. babylonica Linn.	...	...	++	...	...	...	
S. caprea Linn.	...	...	+	...	...	...	
S. cinerea Linn.	...	...	+++	++	+	...	
S. elaeagnos (=*incana* Schrank)	...	...	++	–	+	...	
S. lanata Linn.	+++?	Staining faint except in the cork	+	...	...	...	
S. purpurea Linn.	+	In cork and a few cells in pith	...	...	...	...	
S. triandra Linn.	+	In cork and a few cells in pith	...	...	...	...	
S. viminalis Linn.	+	In cork and a few cells in pith	...	...	...	...	
Santalaceae							
Osyris abyssinica Hochst.	+++	Cortex, phloem, rays, pith (Museum specimen)	...	...	...	...	L. of *Colpoon compressum* Berg. (=*Osyris compressa*), Cape sumac, used loc. Other spp. rich in tannin
O. arborea Wall.	+++	Cortex, phloem, pith (Museum specimen)	...	...	...	...	
Santalum album Linn.	...	...	–	–	–	...	
Thesium humifusum Linn.	–	...	–	–	–	...	

Sapindaceae							
Alectryon excelsum Gaertn.	++	Cork, cortex, phloem, pith	+	–	++	...	Pods of *Paullinia cupana* H. B. & K., 'guarana', used. B. of *Schleichera oleosa* Merr. has been used loc. Other spp. rich in tannin. (Condensed)
Dodonaea viscosa Jacq.	–	...	+	–	++	...	
Koelreuteria paniculata Laxm.	++	Cork, cortex and phloem	++	+	+	...	
Nephelium longana Cambess.	++	Cork, phloem, rays, pith	...	...	...	...	
N. tomentosum F. Muell.	...	...	+++	+	++	...	
Xanthoceras sorbifolia Bunge	+	Abundant in cork; a little in pith	+++	+	(+)	...	
Sapotaceae							
Achras sapota Linn.	++	Cork, cortex, phloem, rays, pith	...	++	–	...	*Imbricaria maxima* Poir., *Chrysophyllum glyciphloeum* Casar., *Madhuca* (=*Bassia*) spp. etc. used loc.
Argania sideroxylon Roem. & Schult.	+	Mainly phloem and pith	+	+	–	...	
Mimusops elengi Linn.	++	Cork, cortex, phloem, pith	++	++	+	...	
Pouteria suavis Hemsl.	+	Generally distributed	(+)	(+)?	–	...	
Sarraceniaceae							
Sarracenia purpurea Linn.	++	Mesophyll, phloem, etc. (leaf)	+	–	+	...	...
Saurauiaceae							
Saurauia subspinosa Anthony	+	In cork and scattered cells	++	–	+	...	...
Saururaceae							
Houttuynia cordata Thunb.	+	Scattered cells	...	...	...	...	...
Saururus cernuus Linn.	...	...	++	–	++	...	...
Saxifragaceae							
Astilbe simplicifolia Mak. var. *rosea* Ahrends	...	...	++	–	++	...	Badan (a mixed tannin) from *Bergenia crassifolia* Fritsch and other spp. 'Encino' from b. of *Weinmannia* spp. Other spp. used loc.
Bauera rubioides Andr.	...	...	++	+	–	...	
Bergenia crassifolia Fritsh (=*Saxifraga crassifolia* Link)	...	...	++	...	...	...	
B. delavayi Engl.	+	Few scattered cells	...	...	...	...	
Boykinia aconitifolia Nutt.	...	...	++	–	++	...	
Francoa ramosa D. Don	...	...	–	–	–	Ellagic +	
Heuchera americana Linn.	+	Scattered cells	...	...	...	...	
H. macrophylla Lodd. ex G. Don	+	Scattered cells	...	...	...	...	
Saxifraga fortunei Hook.	(+)?	Scattered cells; staining not pronounced	...	...	...	...	
Schisandraceae							
Illicium floridanum Ellis	...	...	+++	+	++	...	...
I. verum Hook. f.	++	Abundant in cortex and phloem	...	...	...	...	...
Kadsura japonica Juss.	++	Abundant in cortex and phloem	++	++	+	...	...
Scrophulariaceae							
Antirrhinum majus Linn.	–	...	×	–	–	Dk. brown	...
Dermatobotrys saundersii Bolus	–	...	×	–	–	Dk. rose → grey-brown	...
Diascia barberae Hook. f.	–	...	×	–	–	Dk. purplish brown	...
Digitalis purpurea Linn.	–	..	...	–	–	...	...
Hebe brachysiphon Summerhayes (=*H. traversii*	+	Epidermis	×	–	–	Golden brown	...
Ourisia macrophylla Hook.	–	...	×	–	–	...	...

Table 1 (*cont.*)

	Anatomical data		Chemical data				Recorded occurrence of useful tannins
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	
Scrophulariaceae (*cont.*)							
Paulownia tomentosa (Thunb.) Steud.	(+)?	Possibly trace in cork and phloem	×	–	–	Purplish brown	...
Scrophularia aquatica Linn.	–	...	...	–	–	...	...
Selaginaceae							
Globularia cordifolia Linn.	–	...	...	...	...	...	...
G. vulgaris Linn.	...	...	×	–	–	× Black	...
Simarubaceae							
Ailanthus altissima Swingle	+	Mainly in cork; a little in pith	+	...	...	...	B. of *Simaruba amara* Aubl. used loc.
Solanaceae[1]—entirely negative	...	...	...	...	...	...	...
Stachyuraceae							
Stachyurus praecox Sieb. & Zucc.	++	Abundant in cork; scattered cells elsewhere	++	–	+	Ellagic +	...
Staphyleaceae							
Staphylea colchica Stev.	++	Abundant in cork; some in cortex	...	...	...	...	...
S. coulombieri Éd. André	...	...	++	–	++	...	...
S. holocarpa Hemsl.	+	Mainly in cork	...	...	...	...	...
Sterculiaceae							
Dombeya burgessiae Gerr. ex. Harv.	...	...	++	–	+	...	L. of *Heritiera minor* Lam. important loc.
D. nairobensis Engl.	++	Abundant in cork; elsewhere in scattered cells	...	...	...	...	
Fremontia mexicana MacBride	++	Abundant in cork; elsewhere in scattered cells	++	–	+	...	
Theobroma cacao Linn.	++	Mainly in cork and distal end of rays	+	–	+	...	
Styracaceae							
Halesia diptera Linn.	+	Mainly in cork, but some in scattered cells	–	–	–	...	...
Tamaricaceae							
Tamarix tetrandra Pall. ex Bieb.	+	Mainly in cork; some in scattered cells	–	–	–	...	Galls of *Tamarix aphylla* Lanza and *T. gallica* L. used com. (Constitution uncertain)

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[1] Negative for both tannin and L-A: *Cestrum parqui* L'Hérit., *Cyphomandra betacea* Sendt., *Datura stramonium* Linn., *Fabiana violacea* Hort., *Nicotiana rustica* Linn., *Physalis francheti* Mast., *Solanum dulcamara* Linn., *S. jasminoides* Paxt. Negative for tannin: *Nierembergia coerulea* Gill. ex Miers. (leaf and stem). Negative for L-A: *Nierembergia repens* Ruiz. & Pav.

Tetracentraceae							
Tetracentron sinense Oliver	+	In cork only	+	−	+	...	...
Theaceae							
Camellia cuspidata Hort.	+	Mainly in phloem and rays	+	−	+	Ellagic +	B. of *Gordonia* spp. used loc. Numerous spp. contain tannin
C. japonica Linn.	+ or ++	Phloem, rays, pith. Staining not quite typical	+	−	+	Ellagic +	
Cleyera ochnacea DC.	+	Mainly in cork and phloem	+	−	+	Ellagic +	
Theophrastaceae							
Clavija longifolia Ruiz. & Pav.	+	In b. Staining not typical	−	−	−	...	...
C. ornata D. Don	+	In b. Staining not typical	...	...	...	...	...
Deherainia smaragdina Decne.	+	...	−	−	−	...	...
Thymelaeaceae							
Daphne laureola Linn.	+	Abundant in cork	−	−	−	...	B. of *Daphne gnidium* L., 'garoe', used loc.
Pimelea ferruginea Labill.	+	Chiefly in cork	(+)	...	...	...	
Tiliaceae							
Entelea arborescens R. Br.	+	Scattered cells	+	−	+	...	B. of *Luehea speciosa* Willd. used loc. Other spp., e.g. of *Pentace*, *Sloanea*, contain tannin
Grewia occidentalis Linn.	...	...	+	−	+	...	
G. similis K. Schum.	+	Cork, cortex and pith	...	...	...	...	
G. vernicosa Schinz.	+	Cork, distal ends of rays, and outer pith	...	...	...	...	
Tilia×vulgaris Hayne (=*T. europaea* L.)	++	Generally distributed	+	−	+	...	
Trochodendraceae (see Tetracentraceae for *Tetracentron*)							
Trochodendron aralioides Sieb. & Zucc.	+	Mainly phloem and pith	+	(+)	+	...	...
Tropaeolaceae							
Tropaeolum majus Linn.	−	...	−	−	−	...	...
Turneraceae							
Turnera diffusa Willd. ex Schult. var. *aphrodisiaca*	+	Cork, phloem, pith (Museum specimen)	...	...	...	...	...
T. serrata Vell.	...	...	−	−	−	...	...
T. ulmifolia Linn.	+	In cork and in scattered cells	...	...	...	...	...
Ulmaceae							
Ulmus procera Salisb.	+	Cork, phloem, rays and outer pith	++	−	+	...	...
Umbelliferae —all negative except:							
Bupleurum fruticosum Linn.	(+)	In cork	−	−	−	...	...
Urticaceae							
Boehmeria nivea Gaudich.	(+)?	Staining not convincing	(+)	...	...	...	...
B. platanifolia Franch. & Sav.	...	...	++	−	++	...	...
Parietaria diffusa Mert. & Koch	(+)?	Staining not convincing	++	...	...	...	...
Pilea muscosa Lindl.	(+)	Mostly in phloem	+	−	+	...	...
Urtica dioica Linn.	(+)	In the phloem	−	−	−	L-A (+) in stem	...

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[1] Negative for both tannin and L-A: *Aegopodium podagraria* Linn., *Eryngium campestre* Linn., *Foeniculum vulgare* Mill., *Myrrhis odorata* Scop., *Smyrnium olusatrum* Linn.

Table 1 (*cont.*)

	Anatomical data		Chemical data				Recorded occurrence of useful tannins
	Tannin	Notes	L-A reaction	L-D	L-Cy	Notes	
Vacciniaceae							
Agapetes macrantha Benth. & Hook.	+ or ++	Cork, phloem, distal ends of rays	++	–	++	...	...
Macleania punctata Hook.	++	Cork, phloem, rays and outer pith	+	–	+	...	...
Pentapterygium serpens Klotzsch	+	Mainly cork and phloem	+	–	+	...	...
Valerianaceae[1]—entirely negative	...	...	...	...	...	...	...
Verbenaceae							
Avicennia nitida Jacq.	+	Epidermis of very young stem	–	–	–	...	*Avicennia marina* Vierh. and *A. nitida* Jacq. constituents of mangrove (cf. Rhizophoraceae). L. of *Vitex divaricata* Sw. used loc. (Constitution unknown)
Callicarpa japonica Thunb.	–	...	–	–	–	...	
C. purpurea Juss.	...	...	–	–	–	...	
Caryopteris clandonensis Hort.	...	...	×	...	...	Brown	
C. tangutica Maxim.	–	...	×	...	...	Purplish brown	
Clerodendron fargesii Dode	–	...	–	–	–	...	
Diostea juncea Miers	–	...	–	–	–	...	
Duranta plumieri Jacq.	–	...	–	–	–	...	
Petrea volubilis Linn.	–	...	–	–	–	...	
Tectona grandis Linn.	–	...	×	...	...	Brown-scarlet	
Violaceae[2]—entirely negative	...	...	...	...	...	...	...
Vitaceae							
Leea angulata Korth. ex Miq.	++	Cortex, phloem, pith	...	...	...	...	Seeds of *Vitis vinifera* L. said to have been used
L. coccinea Planch.	...	...	+	+	+	...	
Vitis vinifera Linn.	++	Phloem, rays and outer pith	++	+	+	...	
Winteraceae							
Drimys winteri Forst.	(+)?	Staining not very definite	+	–	+	...	...
Zygophyllaceae							
Zygophyllum fabago Linn.	–	...	–	–	–	...	...

[1] Negative for both tannin and L-A: *Centranthus ruber* DC., *Valeriana officinalis* Linn. Negative for tannin: *Valeriana sambucifolia* Mikan.

[2] Negative for both tannin and L-A: *Melicytus ramiflorus* Forst., *Viola odorata* Linn. Negative for tannin: *Hymenanthera obovata* T. Kirk. Negative for L-A: *Hymenanthera chathamica* T. Kirk.

Malvaceae, where there is marked variation in tannin reaction from one member to another.

It seems probable that these two causes taken together would bring the degree of congruence between the two lists to not far short of 90 %. There are two other circumstances which account for a considerable part of the remaining discrepancy.

(iii) *Presence of ellagitannin.* Ellagic acid was found to be present in the leaves in eighteen cases (3·3 %) in which, while tannin was recorded in the stems, L-A was absent.

(iv) *Constituents not of tannin nature which react with the staining reagent.* Examples in which this may provide an explanation of discrepancy are those of mucilage in Boraginaceae, and aucubin-like substances in Scrophulariaceae. Constituents of as yet unknown constitution may be responsible for positive reactions in a few members of Compositae, Oleaceae, etc.

Significance of leuco-anthocyanin type

Leuco-delphinidin (L-D), when it occurs, usually occurs along with leuco-cyanidin (L-Cy), but often the latter is the only type present. With the larger number of results now available, it is easier to discern a regularity in the distribution of the L-A types than was previously possible (Bate-Smith & Lerner, 1954).

The families in which L-D occurs are found mainly in the Benthamian orders Guttiferales, Celastrales, Sapindales, Rosales, Myrtales, Ericales, Daphnales, Primulales and Ebenales; and in the series Unisexuales which includes Euphorbiaceae, Platanaceae, Casuarinaceae, Betulaceae, Corylaceae and Fagaceae. Those in which L-Cy alone occurs are fairly closely confined to Ranales, Malvales and Geraniales (the latter including many ellagic acid types); but also in such scattered families as Sarraceniaceae, Nepenthaceae, Pittosporaceae, Rosaceae (excluding Chrysobalanoideae), Staphyleaceae, Salicaceae, Begoniaceae, Urticaceae (*sensu lato*) and Empetraceae.

The position of ellagic acid (E), considered in relation to that of L-D and L-Cy, is interesting and revealing. It is well illustrated in the case of the Myrtales. The tannins present in the families of this (Benthamian) order are as follows:

Myrtaceae		L-D	E	L-Cy	generally
Lecythidaceae	from	L-D	E	L-Cy	to E only
Melastomaceae	from	L-D	E	L-Cy	to E only
Combretaceae	from		E	L-Cy	to E only
Rhizophoraceae (*Cassipourea* only)			E		(L-pelargonidin)
Lythraceae			E		
Punicaceae			E		
Onagraceae	from		E		to none

A gradation can be seen from the families whose members are characteristically forest trees and woody lianes, through the typically mangrove families to the largely herbaceous Onagraceae. The gradation is even more evident if other families included by Engler in his order Myrtiflorae are also considered:

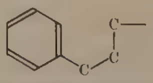
Elaeagnaceae	L-D	E	L-Cy	to E only
Nyssaceae		E		
Haloragidaceae		E	L-Cy	to E only
Hippuridaceae	none			

The progression is, in descending order of woodiness, from a condition in which all the tannin constituents are present, through one in which L-D is absent, then through a condition where ellagic acid only is found, to one in which none are present. This, by and large, is a situation which prevails throughout the whole class of dicotyledonous plants. Often, however, L-Cy occurs throughout a family or order with neither L-D nor ellagic acid anywhere present in the group, and this may mean that the ability to synthesize trihydroxy compounds has been lost at a very early stage in the phylogeny of the group (or, less probably, may never have been acquired).

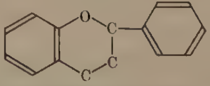
Among the many other particular cases that might be discussed, that of the Rosaceae is outstanding. In the Rosales as a whole, L-D occurs quite regularly and ellagic acid frequently. In the Saxifragaceae (*sensu* Bentham and Hooker), for instance, the situation is very similar to that described for the Myrtales, ranging from *Ribes* with L-D, E and L-Cy to *Francoa ramosa* with E only and *Deutzia setchuanensis* with none. Of the six subfamilies of Rosaceae, three, viz. Spiraeoideae, Pomoideae and Prunoideae (Neuradoideae not examined) contain L-Cy only (but often in very large amount). Rosoideae regularly contain ellagic acid, often with very reduced amounts of L-A (always L-Cy), but Chrysobalanoideae contain both L-D and L-Cy. It is of particular interest to note that it has been suggested that this subfamily should be separated from the remainder of the Rosaceae and given the status of a separate family (Juel, 1915). In Leguminosae-Papilionatae, as previously remarked (Bate-Smith & Lerner, 1954), there is an interesting correlation between the presence of L-A (usually both L-D and L-Cy) and the presence of pulvini. Ellagic acid is only rarely present in this family.

The connexion between tannins and woody habit

The association that exists between the presence of leuco-anthocyanins in the leaves and woodiness in the species or family has been pointed out on previous occasions (Bate-Smith & Lerner, 1954; Bate-Smith, 1956*b*). It is hard to envisage a causal connexion between the presence of leuco-anthocyanins in the leaves and the tendency for other tissues of the plant to become woody, but the gap has been decreased not only by the demonstration of the coincidence between leuco-anthocyanins in the leaves and tannin in the stems of the same plants, but also by the increasing reports of leuco-anthocyanins occurring in woods themselves (cf. Hillis, 1956*a*; Roux, 1956). Even supposing, however, that the specific substances of wood were actually produced from leuco-anthocyanins, it would not be necessary to assume translocation from the leaves in order to account for the presence of those specific substances in the wood; they might arise from leuco-anthocyanins formed in the wood itself by similar processes to those responsible for their formation in the leaves. Nevertheless, in a recent study (Hillis, 1956*a*) of the origin of heartwood constituents, such translocation was regarded as probable. The present results, confirming those reported earlier, indicate that leuco-anthocyanins are not always required to be present in leaves in order that the plant may become woody. The Oleaceae, Buxaceae, Aquifoliaceae, Bignoniaceae and Verbenaceae, as well as certain members of the Bombacaceae, Leguminosae, Fagaceae and Moraceae, provide sufficient evidence of this. Nor is there any obvious route by which leuco-anthocyanins might be supposed to be converted into lignin. In so far as the chemistry of that substance is known, it appears to be composed of phenyl-propane units, for which more obvious precursors than leuco-anthocyanins, which are already condensed into a fifteen-carbon-atom skeleton, can be suggested. It seems more likely that the presence of leuco-anthocyanins is associated with the non-lignin constituents of wood. They are conspicuously present, for instance, in the leaves of trees which form heartwood, and usually absent from those of trees which form only sapwood. The rather indeterminate difference between these two types seems to lie in the weight of phenolic materials of various, and usually unknown, kinds included in the former. Some of these included



Phenylpropane skeleton



Leuco-anthocyanin skeleton

materials provide commercial tannins; an outstanding example is quebracho, from *Schinopsis lorentzii* etc. (Anacardiaceae), but in spite of much work the precise nature of the tannin in this heartwood extract is still unknown. Other tanning materials derived from heartwood, of eucalyptus, for example, contain considerable amounts of leuco-anthocyanins. It seems likely that 'wood' contains and owes its properties to phenolic materials originally identical with those found in the leaves and other living tissues of the plant, but highly concentrated and in a form more or less altered by hydrolysis, oxidation and condensation. Strangely enough, no one seems to have studied the phenolic substances in the *leaves* of the trees, from whose wood and bark most of the world's tanning materials are extracted.

The changes which might take place in leuco-anthocyanins as the sapwood becomes converted into heartwood are such as to increase their molecular size by condensation of unit molecules to one which, while 'permitting suitable solubility in water' (cf. p. 669) also confers the other properties required of tannins, e.g. the ability to precipitate gelatin and alkaloids from solution, and astringency (cf. Bate-Smith, 1954*b*). Monomeric synthetic leuco-cyanidin does not possess these properties in marked degree, but acquires them, apparently as a result of increase in molecular size, when treated briefly in the cold with dilute acid or alkali (Bate-Smith & Swain, 1956). The leuco-anthocyanins from natural sources, even when carefully extracted, are often nearer in properties to this 'polymerized' leuco-cyanidin. Carrying the 'polymerization' further results in insolubility accompanied by darkening in colour to the phlobaphene condition. It seems highly probable, therefore, that the contribution which leuco-anthocyanins make to wood is to the formation of heartwood, and especially by contributing the constituents responsible for the characteristic colour of the heartwood. Thus we find that few of the species from the leaves of which leuco-anthocyanins are absent—e.g. ash, holly—are heartwood trees, and such as are heartwood trees—e.g. hornbeam—have plentiful ellagitannin. The connexion between leuco-anthocyanin in the leaves and woody habit in the plant now becomes more understandable. It is a connexion not with lignification as such, but with the deposition of extractives in lignified tissues as they acquire the heartwood condition. It is impossible to be more definite than this because of the absence of knowledge of the chemistry of the processes concerned in lignification.

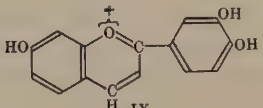
Hillis (1956*a*) suggests that the leuco-anthocyanins in the wood are transported in their low-molecular, water-soluble, form from the leaves. While this is possible, the fact that we find in general a coincidence between the L-A reaction in leaves and the tannin reaction in stems suggests to us that the ability to produce leuco-anthocyanins is common to most tissues of L-A producing plants. Hillis shows that the L-A content of leaves fluctuates markedly with the stages of maturity, but this does not necessarily mean that movement is involved: as he himself points out, substances of the constitution suggested for leuco-anthocyanins are readily convertible by oxidation to flavonols and other flavonoid substances actually known to be present in the leaves along with the leuco-anthocyanins. It seems to us more likely that the leuco-anthocyanins in wood are formed within the living cells of the sapwood, increasing as the cells die and form the heartwood tissue.

Leuco-anthocyanins in commercial tanning materials

Although little attention has been paid to the occurrence of L-A's in tanning materials, it would seem, judging from the data in the last column of Table 1, that there can be few such materials that do not contain, or did not originally contain, L-A's. So far only Hillis (1954, 1956*b*) has critically examined tanning materials for the presence of L-A's. He found them to be present in mallet, red ironbark, red stringy bark, and 'Myrtan' (all from *Eucalyptus* spp.), in mangrove, in wattle (*Acacia* spp.), *Butea frondosa* kino, and radiata pine; but absent from myrobalans (*Terminalia chebula*). His observations agree closely with our own observations of the nature of the tannins in the same or nearly related species.

It is not at present possible to estimate with any accuracy the amount of L-A present in a plant extract: it is only possible to estimate the anthocyanidin formed when the extract is heated with acid, and this varies in an uncertain way with the conditions of treatment and the state of the L-A in the extract. Nevertheless, Hillis's results leave no doubt that the L-A's form a major fraction of many of the extracts he examined and, bearing in mind their tannin-like properties, they may well be expected to contribute to the tanning action of the extracts.

Roux (1956) has recently shown two leuco-anthocyanins to be present in quebracho extract, the predominant one yielding an anthocyanidin of the structure IX when heated with hydrochloric acid. This corresponds in its hydroxylation pattern with the flavonol fisetin, which occurs in quebracho (Kirby & White, 1955), just as cyanidin (I) and delphinidin (II) correspond with the more commonly occurring flavonols quercetin and myricetin. An L-A yielding IX has also been found in the heartwood of the black wattle (*Acacia mollissima*) (Keppler, 1956).



IX

One of the greatest puzzles is what kind of substances are responsible for the tanning action of the verbenaceous extracts, *Avicennia nitida* and *Vitex divaricata*. None of the Verbenaceae examined contain catechins, leuco-anthocyanins, gallic acid, or ellagic acid, and all were negative for microscopical tannins except that a little tannin has been detected microscopically in the epidermis of very young stems of *Avicennia nitida*. In spite of the small amount of tannin which has been detected in *A. nitida*, it is one of the mangrove species of which the tannin extract is important commercially.* Although *Vitex divaricata* has given wholly negative results in our tests, it is reported to contain 14% of tannin. These materials would obviously repay closer study.

CONCLUSIONS

(*a*) *Tannin synthesis and taxonomy*

In the remarks which follow concerning the occurrence of tannins which have been examined microscopically, it must be remembered that we are referring to young shoots. Although our investigations have shown that when tannins occur in the young stem they can usually be detected chemically in the leaves also, it does not necessarily follow that tannins will inevitably be present throughout the plants. We have made no observations on roots, fruits or seeds during the present investigation.

The results of this investigation show conclusively that dicotyledonous families fall into three groups. First, there are the families in which all, or nearly all, of the species that have been examined are capable of synthesizing substances that the microscopist would refer to loosely as tannins. Then there is a second group of families in which the presence of tannins has not been demonstrated, or in which they are present to a very limited extent. Between these two extreme types there is a third group of families for which very mixed results have been obtained. The following alphabetical lists indicate which are the highly tanniniferous and non-tanniniferous, or only slightly tanniniferous families respectively, and it can be assumed that any of the other families which we have examined have given mixed results.

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* *Added in proof*. We are informed by Dr W. E. Hillis that there is, in fact, some doubt regarding the use of this species in the preparation of mangrove cutch.

(1) *Families in which all of the species examined are tanniniferous*

Families included in this category are those in which all of the species examined have been found to contain tannins that can be demonstrated microscopically, or tannin-like substances which can be detected by the chemical tests which we have employed. In many, but not all, of the species tannins have been detected both microscopically and chemically.

Aceraceae, Actinidiaceae, Anacardiaceae, Annonaceae, Balsaminaceae, Begoniaceae, Betulaceae, Bixaceae, Casuarinaceae, Cercidiphyllaceae, Cornaceae, Clethraceae, Corylaceae, Corynocarpaceae, Cunoniaceae, Daphniphyllaceae, Diapensiaceae, Dilleniaceae, Droseraceae, Ebenaceae, Elaeocarpaceae, Ericaceae, Erythroxylaceae, Escalloniaceae, Eucommiaceae, Eucryphiaceae, Eupomatiaceae, Fagaceae, Frankeniaceae, Grossulariaceae, Guttiferae, Haloragaceae, Hydrangeaceae, Hypericaceae, Juglandaceae, Lardizabalaceae, Lauraceae, Limnanthaceae, Lythraceae, Magnoliaceae, Melastomaceae, Meliaceae, (Monimiaceae), Moraceae, (Myoporaceae), Myricaceae, Myrsinaceae, Myrtaceae, (Nepenthaceae), (Nyssaceae), (Onagraceae), (Oxalidaceae), Plumbaginaceae, Polygonaceae, Proteaceae, Punicaceae, Rhizophoraceae, Rosaceae, Sabiaceae, Sapindaceae, Sapotaceae, Sarraceniaceae, Saurauiaceae, Saururaceae, Saxifragaceae, Schisandraceae, Simarubaceae, Stachyuraceae, Staphyleaceae, Sterculiaceae, (Styracaceae), (Tamaricaceae), Tetracentraceae, Theaceae, (Thymelaeaceae), Tiliaceae, (Trochodendraceae), Ulmaceae, Urticaceae, Vacciniaceae, Vitaceae, Winteraceae.

(2*a*) *Families which gave mostly negative results*

Araliaceae, Aristolochiaceae, Asclepiadaceae, Bignoniaceae, Compositae, Leguminosae-Papilionatae, Nyctaginaceae, (Nymphaeaceae), (Oleaceae), Piperaceae, Ranunculaceae, (Scrophulariaceae), Umbelliferae.

(2*b*) *Families which gave completely negative results*

Acanthaceae, Amaranthaceae, Basellaceae, Buxaceae, Cactaceae, Campanulaceae, Capparidaceae, Caryophyllaceae, Chenopodiaceae, Chloranthaceae, Cneoraceae, Convolvulaceae, Cruciferae, Cucurbitaceae, Datiscaceae, Dipsacaceae, Ficoidaceae, Fumariaceae, Garryaceae, Gesneriaceae, Hippuridaceae, Hydrophyllaceae, Labiatae, Lentibulariaceae, Linaceae, Loasaceae, Papaveraceae, Phytolaccaceae, Plantaginaceae, Polygalaceae, Portulacaceae, Resedaceae, Solanaceae, Tropaeolaceae, Valerianaceae, Verbenaceae, Violaceae, Zygophyllaceae.

Perusal of these three lists shows that each of them includes representatives of a very miscellaneous collection of families. Nevertheless, an attempt has been made to determine whether a high proportion of the families in each of the lists fall into, or are characteristic of, any particular orders of families recognized in the respective systems of Bentham and Hooker, Engler, and Hutchinson. It is well known that the number and composition of the orders in each of these systems differ considerably, so it is not surprising to find that there is no very close concordance between the families in the three lists given above and orders that are common to all three systems. If the lists are considered in relation to the orders in the Engler system, however, some rather interesting points emerge. Thus of the 38 non-tanniniferous families in list 2*b* it will be noted that 7 belong to the Tubiflorae, 7 to the Centrospermae, 5 to the Rhoeadales, 5 to the Geraniales, 3 to the Parietales, 2 to the Rubiales, and 1 each to the Garryales, Sapindales, Opuntiales, Campanulatae, Piperales, Cucurbitales, Rubiales, Myrtiflorae and Plantaginales.

Some of these orders are relatively small, the Centrospermae consisting of 9 families, the Rhoeadales of 6, the Piperales of 4, and the Opuntiales, Cucurbitales, and Plantaginales of 1 family each. It would thus appear that, on the whole, these orders tend to be non-tanniniferous. Others of the orders concerned are much larger, the Parietales including 29 families, the Sapindales 21, the Geraniales 20, and the Myrtiflorae 19. It thus follows that only a small proportion of the plants belonging to these larger orders are non-tanniniferous. This is correlated with the very heterogeneous composition of the orders in question. Thus, to take but one example, the non-tanniniferous Hippuridaceae of list 2*b* are very unlike the highly tanniniferous Nyssaceae, Punicaceae, Rhizophoraceae and Myrtaceae of list 1, although all of these families belong to the same order.

Of the 13 families in list 2*a* that gave results that are mostly negative, 2 each belong to the relatively small orders Umbelliflorae and Contortae and 1 each to the small orders Aristolochiales and Piperales. The remaining families in this list belong to different orders that are mostly moderately large or large, so that the orders include no more than a very small percentage of non-tanniniferous species. The relatively small orders Umbelliflorae, Aristolochiales and Contortae, on the other hand, are more completely non-tanniniferous.

We now come to list 1 which is longer than the others and includes 82 highly tanniniferous families. Here it may first be noted that, for the most part, the families are in different orders from those to which the families in lists 2*a* and 2*b* belong. Thus we have 5 in Ericales, 3 in Ebenales, 3 in Malvales, 3 in Sarraceniales, 3 in Urticales, 2 in Fagales, and 1 each in Juglandales, Myricales, Primulales, Plumbaginales, Polygonales, Proteales and Rhamnales, none of which include families in lists 2*a* and 2*b* respectively. Furthermore, these families comprise a fairly high proportion, or the whole, of the orders concerned. Thus the Ericales comprises 6 families, the Ebenales 4, Malvales 8, Sarraceniales 3, Urticales 3, Fagales 2, and the Juglandales, Myricales, Primulales, Plumbaginales, Polygonales, Proteales and Rhamnales 1 each. It may thus be concluded that there is a tendency for these orders to be tanniniferous.

Some of the other families in list 1 belong to orders that include a few of the families in lists 2*a* or 2*b*. Thus, for example, we have, in list 1, 14 out of the 29 families that comprise the Parietales, whilst 3 other families belonging to the same order are amongst the non-tanniniferous families in list 2*b*. This would appear to suggest that the Parietales includes a miscellaneous collection of families that have reached different stages in the evolution of their capacity to synthesize tannins. The same may be said of the Ranales as understood in the Englerian system, for there are 9 tanniniferous Ranalian families in list 1 and 2 Ranalian families that are almost non-tanniniferous in list 2*a*. Here again the reason appears to be that the Englerian concept of the Ranales is at fault, for it includes families that have become widely separated in Hutchinson's system. Hutchinson's narrower concept of the Ranales seems to fit in with the cleavage that is suggested by the occurrence of tanniniferous substances, for his Ranales comprise the Ranunculaceae and Nymphaeaceae, the 2 Ranalian families in list 2*a*, together with the Cabombaceae and Ceratophyllaceae which were not examined during the present investigation. The 9 tanniniferous Ranalian families in list 1 are included amongst Hutchinson's orders Annonales, Berberidales, Laurales and Magnoliales which he does not regard as being closely related to the Ranales in a narrow sense.

These results, taken collectively, show that the capacity for Dicotyledons to synthesize tannins has been evolved in a manner that corresponds to quite a marked extent with our present concepts concerning the composition of families. There are also some points of agreement between the arrangement of families in orders and their capacity to synthesize tannin. That this agreement would prove to be no greater might have been expected from the very fact that there are marked differences of view in each of the leading systems of classification, concerning the composition of orders.

(*b*) *Tannin synthesis and phylogeny*

Since tannin synthesis is much more marked in some families than in others it is reasonable to inquire if there is any relationship between the formation of these substances and the phylogenetic status of the families in which they occur. This question is very difficult to answer because there is no general agreement concerning the phylogeny of the angiosperms, many of the views on this subject that have been expressed resting on personal, although for the most part intelligent and authoritative, conjecture. There is, however, the statistical approach to this problem that has been developed by Sporne (1954), who has attempted to reduce 'to mathematical terms the discussion of evolution in large groups of organisms, thereby avoiding, as far as possible, the effects of personal bias'. As a result of his investigations, Sporne has arranged most of the commonly recognized families of dicotyledons in an ascending phylogenetic series, the position of each family in the series being designated numerically by an 'advancement index', the most primitive being those families whose advancement index is nearest to zero and the most advanced are those with an index of 100.

Whilst Sporne's results include a few that seem rather surprising, and, indeed, on the face of things rather improbable, his advancement index, taken as a whole, does provide a phylogenetic yardstick of considerable value. It seems that, in at least certain instances, the more doubtful results obtained by Sporne occur where he is dealing with large assemblages that are commonly treated as if they were families, but which are, in reality, more in the nature of orders. For example, the Leguminosae which appear with the surprisingly low advancement index of 18. This is in spite of the fact that at least certain of the woody Leguminosae exhibit short barrel-shaped vessel members and storied wood, both of which characters are regarded by wood anatomists as highly advanced. On the other hand, it must at once be admitted that many other Leguminosae are far from having reached this high level of structural specialization in the wood. It is thus clear that within the Leguminosae as a whole there is a very considerable range of specialization, such as might be found in an order, and the advancement index of 18 scarcely indicates what is the true state of affairs for the group as a whole. This, indeed, has been confirmed for us by Dr Sporne (personal communication) in a provisional estimate he has made of the advancement index of each of the three subfamilies of Leguminosae: Mimosoideae 17, Caesalpinioideae 21, Papilionatae 29. Then again we find the Euphorbiaceae with a low advancement index of 25. This can scarcely be applicable to the whole of the vast assemblage of plants that constitutes the Euphorbiaceae, a group exhibiting a very wide range of habit forms and histological characters, and one which some botanists, with good reason, believe to be artificial.

These, and other recognized difficulties in Sporne's phylogenetic hierarchy, must not blind us to the fact that it may, in a general way, present an approximation to phylogenetic truth. With this possibility in mind, the families in the three lists have been marked, as far as possible, with the advancement index numbers that have been assigned to them by Sporne. The result is at least full of interest. Thus the advancement index numbers of the 82 tanniniferous families in list 1 lie between 14 and 75, only 24 being over 50. The index numbers for the 13 almost non-tanniniferous families in list 2*a* lie between 32 and 93, only 4 being below 50. Finally the index numbers for the 38 non-tanniniferous families in list 2*b* lie between 36 and 100 with only 8 below 50. These facts indicate conclusively that the capacity to synthesize tannins decreases as the advancement index numbers for the families go up. It thus seems that the capacity to synthesize tannin is a primitive character that tends to become lost with increasing phylogenetic specialization. Furthermore, as indicated on p. 698, this absence or reduction of tannin production is often, but not invariably, most marked in herbaceous rather than woody plants. Facts such as these show how useful comparative biochemistry may become in the study of phylogeny, but it is clearly evident that the results are likely to be most fruitful when the biochemist works in collaboration with the anatomist and taxonomist.

SUMMARY

1. The stems of more than 500 species of dicotyledonous plants from 175 families have been examined histologically, using sections fixed in formalin-acetic-alcohol and in which the tannins have been made conspicuous by iron salts. The leaves of the same or nearly related species have been examined chemically for leuco-anthocyanins. In 83 % of the cases the presence or absence of tannins in the stems coincides with the presence or absence of leuco-anthocyanins in the leaves. It is therefore suggested that the histological reaction for tannins is most commonly due to leuco-anthocyanins.

2. In about one-fifth of the cases where agreement has not been observed, ellagic acid is present in the leaves and it is presumed that ellagitannins are responsible for the staining reactions observed in the stems. In other instances, e.g. *Cornus*, *Sambucus*, *Passiflora*, leuco-anthocyanins, although absent from the leaves, are present in the stems. The remaining cases are accounted for either by dissimilarity of the species examined (e.g. Santalaceae) or by the presence of constituents which might react with the iron salts although not of tannin nature (e.g. mucilage in Boraginaceae and aucubin-like substances in Scrophulariaceae).

3. The tendency of leuco-anthocyanins and other tannins to be more frequently present in woody plants is confirmed and its significance discussed.

4. The occurrence of tannins can be used as a taxonomic character, for although these substances are of very widespread occurrence amongst the Dicotyledons, some families are highly tanniniferous, in others little or no tannin has been detected, and a third group of families have given mixed results.

5. Some of the orders of Dicotyledons, as understood in the Englerian system, tend to produce tannins more freely than others, but there is no more than a limited agreement between the occurrence of tannins and the composition of the orders as understood in any of the well-known systems of classification.

6. A very interesting parallelism has been noted between the occurrence of tannins and the phylogenetic status of the families in which they occur as revealed by the 'advancement index' assigned to them by the statistical technique developed by Sporne. The capacity to synthesize tannins seems to decrease as the advancement index increases.

The assistance of the Director and Staff of the University Botanic Garden, Cambridge, in supplying botanical material is gratefully acknowledged. Thanks are also due to the gardens staff at Kew for their collaboration in growing and collecting botanical material. So far as one of us (E. C. B-S.) is concerned, the work described in this paper was carried out as part of the programme of the Food Investigation Organization of the Department of Scientific and Industrial Research.

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The vegetation of Socotra. By G. B. Popov, Desert Locust Survey, Nairobi.

(Communicated by Dr B. P. Uvarov, C.M.G., F.R.S., F.L.S.)

(With Plates 55–59 and 1 Map)

[Read 24 May 1957]

Introduction

The existing literature on the vegetation of Socotra is rather scanty. The island received much attention from the collectors at the end of last and early in this century, when several British and German expeditions visited the island. Important contributions were made to the flora, chiefly by Balfour (1888), Forbes *et al.* (1903) and Vierhapper (1907), but these works only contain general brief descriptions of the physiognomy of the vegetation without an attempt at the classification of vegetation communities or types.

Similar brief references are also found in Engler (1910); and Wettstein (1906), and the available information was used by Pichi-Sermolli (1955) in his review of the plant ecology of arid and semi-arid zones of East Africa.

The present author had an opportunity in 1953 to spend a few weeks on Socotra in connexion with control of the Desert Locust. A general ecological survey of the island was carried out in order to investigate its possible suitability as a habitat of the locust. An account of locusts will be published elsewhere, and a list of Saltatorial Orthoptera of Socotra, with zoogeographical analysis of the fauna, is in the course of publication (Popov & Uvarov, in press).

The plants collected during the visit were first examined by Mr B. Verdcourt of the East African Herbarium, Nairobi, where the duplicates were retained. The original specimens were later presented to the British Museum (Natural History) for final determination by Dr G. Taylor, Miss D. Hillcoat and Mr A. W. Exell. The names of plants referred to in this paper were subsequently checked by Mr J. B. Gillett of Royal Botanic Gardens, Kew, who also compiled the list on pp. 717–20. The author wishes to offer his sincere thanks to the above and to Dr B. P. Uvarov for editing this paper.

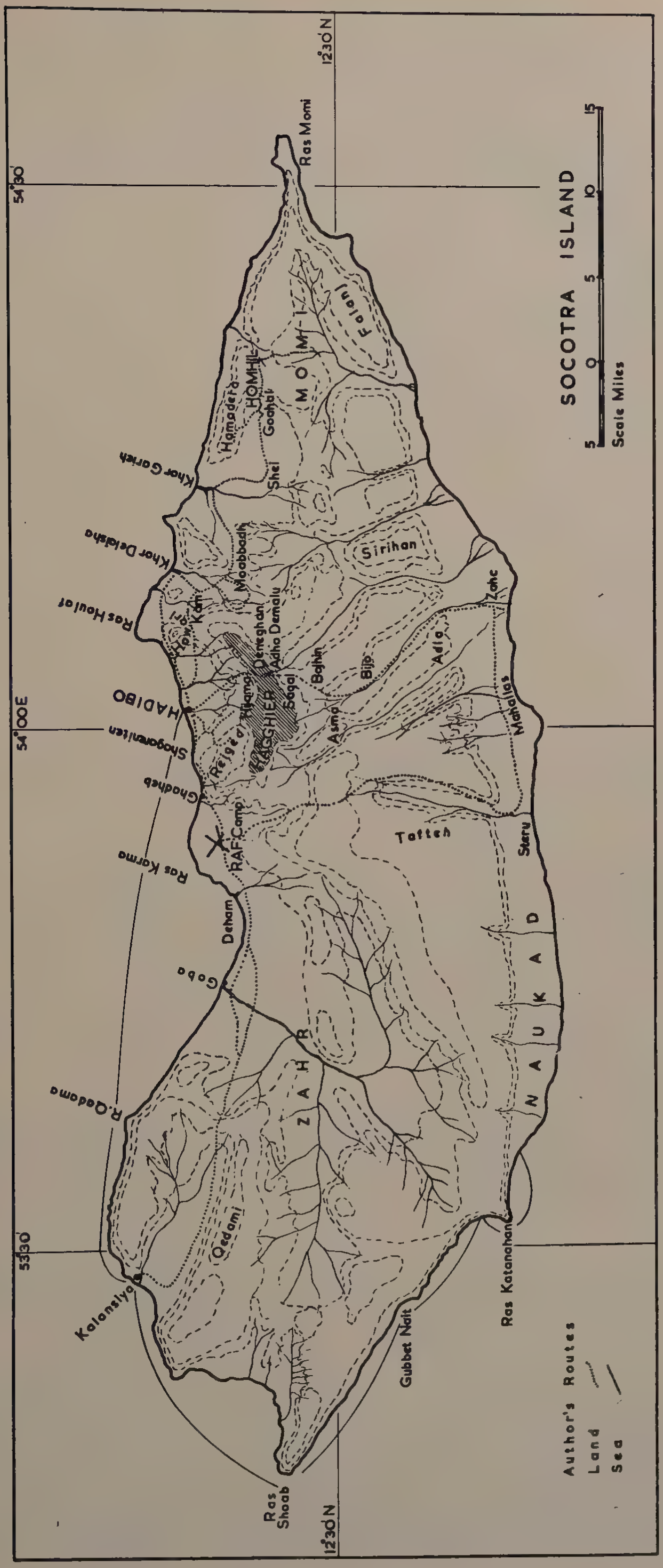
Physical geography and soils

The coastal plains. The southern coastal plain of Naukad is the largest on Socotra, being some 30 miles long and up to 5 miles wide. To a large extent it is covered with packed gravels, stones and coarse sand, with an overlying mantle of loose sand. The loose sand belt runs in a ribbon along the widest part of the plain, locally developing into wind-blown crescentic dunes up to 7 m. high (Pl. 55, fig. 1). This sand has been largely formed through the decomposition of granites, while the beach sands, formed all along this plain, are mainly of shell and coral origin.

The watercourses traverse the plain along single, well-defined beds of boulders and rock slabs, without extensive fanning out or leaving finer deposits. The banks are hardly ever more than 1 m. high, in parts exposing recent conglomerates and raised coral beaches.

Clay and silt deposits are found along some depressions, such as at Mahallas, where the soil is somewhat saline, or in very small quantities along the minor watercourses which, on being blocked by sands, spill and dry up over the plain.

Elsewhere, the southern coastal plain is narrow, and much of the southern coast presents spectacular abrupt cliffs and bluffs, rising steeply to the plateau above. These cliffs are honeycombed with caves and fissures and there is some water seepage, which forms tufa encrustations and deposits in many parts of the cliffs.



Socotra Island

Between Ras Shoab and Katanahan there is a narrow inland basin at Nait separated from the sea by a line of dunes, but filling up at spring tides. The water gradually evaporates, leaving a salt deposit, which is the main source of salt on Socotra. Similar basins are said to exist in other parts of the island, as at Ras Bishuri, near Kalansiya.

The northern coast is composed of a number of smaller coastal plains, separated from each other by rocky headlands. Kalansiya, Goba (Karma) and Hadibo plains are open to the sea and correspond to the bays of the same name. Eastwards from Houlaf to Momi, the lowland plains are separated from the sea by ranges of hills and divided by watersheds into series of small river basins reaching the sea through narrow gorges; Kam, Moabbadh and Khor-garieh are the major ones. From Hamadera to Ras Momi, the coast is again formed by precipitous cliffs.

Much of the soil of the northern coastal plains, like that of Naukad, is composed of packed gravel, stones and coarse sand, with a small admixture of clays. There are some deposits of soft sand, on the Goba plain as thin sheets or hummocks under vegetation, but at Houlaf reaching an unexpected thickness, covering the Houlaf promontory on the one hand, and encroaching on to the seaward slope of Hawari hill to a height of 100 m. or so, on the other (Pl. **55**, fig. 2). It might be more than a coincidence that *Acacia edgeworthii* forms an association in this area, but is rare elsewhere.

A feature common to the greater majority of the northward draining watercourses of Socotra is the formation of estuaries, separated from the sea by sand-bars, which are broken only by the heavy floods. The beds of rivers are covered by stones and boulders most of the way across the plain, but finer soils become deposited at the estuaries, where agriculture is practised. Even here the depth of the soil is so slight, that it is not sufficient to take the full roots of the date palm, which on reaching the rock bed begin to arch and bulge above the soil level.

The large river basin of Zahr was only seen from the air. No large sand deposits were noticed, and in general appearance this area was similar to the coastal plain at Kalansiya. The vegetation is probably akin to that of the coastal zones and not of the limestone plateau proper.

The limestone plateau. This forms the greatest area of Socotra and varies in height between 300 and 700 m., but in places, such as Reiged, rising to 900. Within the confines of the limestone plateau, soil deposits are nowhere great. This area is much dissected by gullies and ravines, and the surface worn smooth or pot-marked by erosion. Little pockets of fine, grey clayey soil occur in the hollows and between rock crevices, but locally larger shallow soil deposits become accumulated in depressions, where the gradient is slight. The largest of these were seen at Homhil, on the summit of Reiged and the plateau of Momi.

The granite highlands. The decomposition of granites, of which the Hagghier Massif is built, has led to the formation of rich red soils. These have become accumulated in the valleys and the plains and even along the less steep slopes, to form the deepest and most fertile soil deposits on Socotra.

CLIMATE

The climate of Socotra is tempered considerably by the north-east and the south-west monsoons and is less torrid than that of the adjacent mainlands. The temperatures recorded by me in spring, 1953, on the coast at Hadibo were: January, mean 24, maximum 30, minimum 15·5; February, mean 25, maximum 31, minimum 16·5; March, mean 26·5, maximum 32·2, minimum 18·3° C. The relative humidity during this period varied from 75 to 90% in the morning and from 55 to 75% at midday. Occasionally even higher humidity was recorded and morning dew was of frequent occurrence. Higher temperatures were experienced in some of the valleys in the lowlands, and they were usually associated with lower humidity. The highest recorded temperature was 35° C. At higher altitudes, particularly in the Hagghier highlands, temperatures were noticeably lower, particularly at night and a minimum of 13·5° C. was recorded at Adho Demalu (1000 m.) in late March. Frost, however, is unknown to the inhabitants.

May is said to be the hottest month, when heat and humidity rise during the period of calms between the monsoons. Later, the heat is relieved by the south-west monsoon, but the high winds are dry and cause desiccation, seldom bringing rain. September is another period of calm airs and high humidity, which ends with the onset of the north-east monsoon, blowing until early May and bringing the main rain to Socotra, with the highest precipitation in November and December.

Table 1 is compiled from rainfall figures recorded by the Royal Air Force Station at Ras Karma, the only locality on Socotra where regular weather observations have been maintained. These figures can be regarded as representative of the amount of rainfall that can be expected in the drier parts of the island. Rainfall is said to be greater in the eastern part of Socotra than the western and, judging by the vegetation, it is probably higher still in the highlands generally and in the Hagghier particularly where, in addition to the rain, frequent mists and dews occur.

Table 1. *Rainfall records for Ras Karma* (*in mm.*)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1943	tr.	0·1	tr.	tr.	tr.	Nil	Nil	tr.	3·2	3·8	89·6	75·2
1944	4·8	2·1	31·4	tr.	Nil	Nil	0·06	Nil	Nil	4·1	60·2	76·6
1945	3·6	3·5	Nil	Nil	4·3	91·0	tr.	Nil	4·0	21·3	5·5	—

Vegetation

In the following pages the major vegetation communities will be described in turn, then ascribed to the nearest vegetation type outlined by Pichi-Sermolli (1955). There are two fundamental difficulties in fitting the vegetation communities of Socotra into this general classification. The first is due to our comparative lack of knowledge of the climatic and other factors affecting the vegetation of Socotra, which serve as the basis for the major divisions of the vegetation types in other areas. The second is due to the peculiar structure of some of the vegetation communities on Socotra, particularly from the point of view of their physiognomy. Thus the *Croton*-short grass community, so prevalent on Socotra, has no real equivalent in East Africa, and the rock communities do not reach the same development there as they do on Socotra. On the other hand, the *Acacia*-short grass savannah, so common in East Africa, is not represented on Socotra. The classification has therefore not always been obvious, and the Socotran communities have been referred to the one or the other type on the basis of a comparison and the personal acquaintance of the author with the vegetation communities in other parts of East Africa.

The basis used by Pichi-Sermolli for the division of the vegetation of East Africa into two major zones—the arid and the semi-arid—has chiefly been the aridity index.

I am in general agreement with Pichi-Sermolli, who regards the greatest part of Socotra as being within the arid zone, with a narrow semi-arid belt in the upper part of the Hagghier range, but he overstressed the aridity of the island, a point which will be made clear in the following description.

(1) *The coastal plains*

Maritime and halophytic communities

Avicennia marina mangroves occur as local narrow belts at a number of points along the coasts of Socotra. One of these was seen at Gubbet Nait, between Ras Katanahan and Ras Shoab—the locality noted for its salt deposits (p. 708). Here, the salt flats are fringed with a woody salt-bush, *Arthrocnemum* sp.?, followed inland by a sward of coarse, spiky salt-grass, *Heleochloa dura*.

The beach dunes along the southern coastal plain of Naukad are fixed seawards by the same salt-grass (Pl. **55**, fig. 3) and landwards by sea-lavender, *Limonium* spp., and in some places by another salt-loving woody herb, *Atriplex stocksii* forma *sokotrana*; these three plants appear to be frequently associated with sands of coralline or shelly origin.

Tamarix sokotrana is evidently less halophytic than the foregoing species, as it often grows away from the coast in less saline, sometimes gypseous soils. It is most common at Khor Garieh, where it forms a narrow belt along the upper end of the inlet, which is evidently subject to tidal inflows. Elsewhere it is occasional; either as a subdominant within the *Limonium* association or as a rock-plant in some of the inland valleys and gorges, usually on tufa deposits.

Suaeda monoica is another member of the halophytic coastal communities of the Naukad plain, but is really common only at Mahallas, where it fringes the palm groves, on low-lying silty soil. The wiry grass, *Aeluropus* sp., and the beautiful, red-flowered, spreading convolvulaceous herb, *Ipomoea pes-caprae*, occur in small colonies on the beaches, but the rush *Juncus arabicus*, which commonly grows in the brackish estuaries, can also be found in the marshes in some inland areas, where water is quite fresh.

Some other plants such as *Sporobolus spicatus*, *Fagonia socotrana*, *Zygophyllum* sp., *Heliotropium* sp., *Aerva microphylla* and a few others are also tolerant of salt to a greater or lesser extent, though probably not dependent on it. These are common members of mixed xerophytic communities on the coastal cliffs, growing nearest to the edge of the sea.

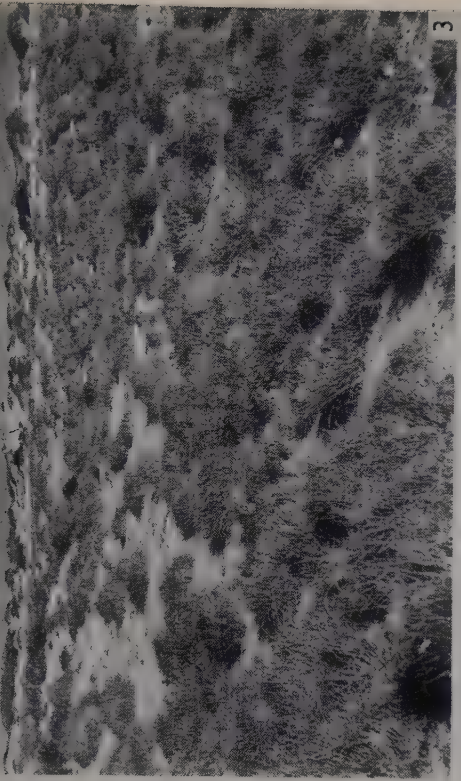
The above-mentioned communities can be directly ascribed to Pichi-Sermolli's type 1, Maritime vegetation (arid zone).

The sand belt

On the southern coastal plain of Naukad many of the dunes are completely devoid of vegetation (Pl. **55**, fig. 1), while others support a thin growth of plants (Pl. **55**, fig. 4; Pl. **56**, fig. 5). No species of plant is evidently confined to this area, though some, e.g. *Calotropis procera*—the large-leaved Asclepiad, are more common here than elsewhere on the island. The perennial plants probably tap the gravel soil below and as such cannot be regarded as truly representative of the sand belt. Among these are *Indigofera* sp.nov.,[1] *I. oblongifolia*, *Ziziphus* sp., *Salsola forskalii*, *Panicum rigidum*, *Corchorus depressus*, *Cucumis prophetarum* and the above-mentioned *Calotropis procera*, which are equally common on the adjoining gravel plain free of surface sand. The numerous annual herbs and ephemerals are probably more representative of sandy soils, where they grow in greater abundance than on the gravel plains. At the time of the visit (March), most of these were already past their prime and the following were recorded as common: *Fagonia paulayana*, *Portulaca quadrifida*, *Dactyloctenium aristatum*, *Phyllanthus* sp., *Heliotropium* sp., *Ageratum conyzoides*, *Boerhavia repens*, *Cenchrus ciliaris*, *Enneapogon* sp. and *Zygophyllum simplex*. As is common in the sandy areas of the adjacent mainlands the community is characterized by nanophanerophytes and ephemerals (Pl. **56**, fig. 5).

Along the northern coast, only at Ras Houlaf are the sand deposits deep enough to affect the vegetation. *Acacia edgeworthii* forms a consociation here, whilst elsewhere it is occasional. The dominant annuals, also largely confined to the sand, being *Dactyloctenium aristatum* and a species of *Cyperus*. The majority of other common plants, however, also occur on the adjoining sand-free, gravelly and stony slopes of Hawari. Of these the most noteworthy are *Indigofera cordifolia*, *I. nephrocarpa*, *I. colutea*, *Seddera latifolia*, *Aerva* sp., *Crotalaria* sp., *Tribulus terrestris*, *Lindenbergia sokotrana*, *Ruellia* sp. and *Arnebia hispidissima* (Pl. **55**, fig. 2).

[1] '*intricata* Boiss.' in the sense of Balfour, Bot. Socotra, *Trans. R. Soc. Edinb.* **31**, 74 (1888), not of Boissier, *Flora Orientalis* **2**, 190 (1872). To be described shortly by J. B. Gillett.



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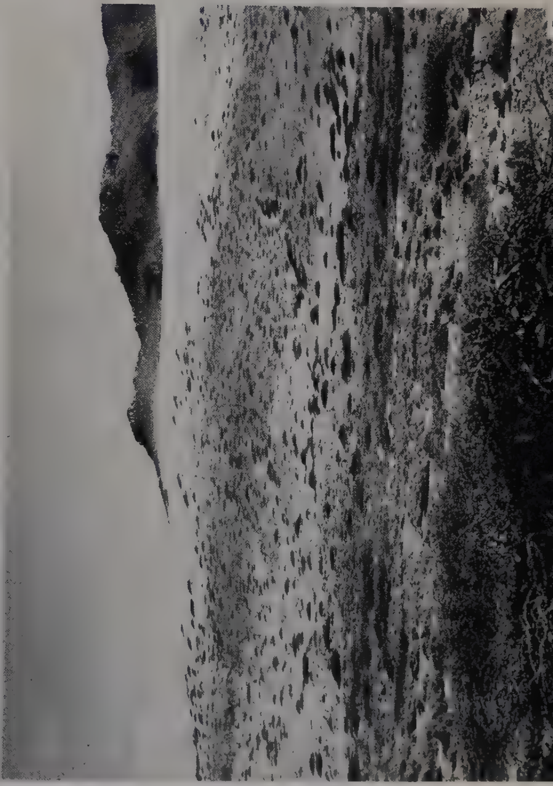
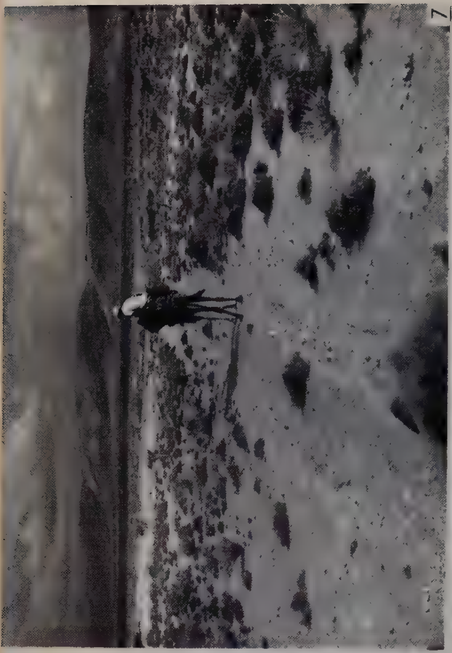


Figs. 1–4. Explanation of Plate on p. 720.

(*Facing p.* 710)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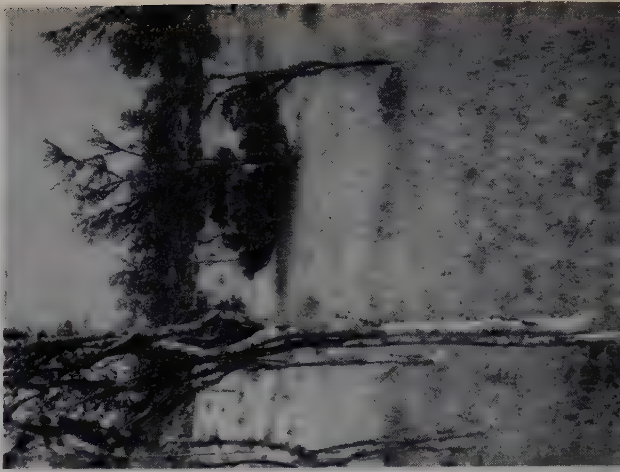

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Figs. 5–8. Explanation of Plate on p. 720.

Coarse sand, gravel and stony plains

The first vegetation zone inland from the sea is formed by the woody herb community (nanophanerophytes). At Hadibo the dominant species is *Indigofera* sp. nov., frequently associated with other woody herbs such as *Convolvulus fastigiatus*, *Campylanthus spinosus*, the tussocky grass *Hyparrhenia hirta*, some annual herbs, *Tephrosia apollinea*, *Aerva javanica*, *Farsetia longisiliqua* and a carpet of ephemeral short grasses, *Aristida adscensionis* and *Melanocenchris abyssinica* (Pl. **56**, fig. 6). Along the river basins east of Houlaf, this community is but poorly represented, but some of its elements occur within the shrub zone (see below). Between Ghadheb and Kalansiya, however, it is well developed, reaching a width of up to 3 km. on the Goba plain.

Other common nanophanerophytes in this area are *Bidens biternata*, *Aerva microphylla*, *Dactyloctenium hackelii*, *Panicum rigidum*, *Euphorbia spiralis*, *E. septemsulcata* and a dwarf *Commiphora*; each of these plants being sometimes dominant locally but rare or even absent elsewhere (Pl. **56**, fig. 7).

In addition, *Aloe perryi* and *Euphorbia arbuscula* form local isolated communities in some areas, while occasional bushes of *Salvadora persica*, *Acacia edgeworthii* and *Cadaba rotundifolia*, usually growing close to the seashore, are conspicuous by their larger size.

Inland this belt is followed by the shrub zone dominated by 'Metred', *Croton socotranus*, which is easily the commonest shrub on Socotra. Sometimes it forms almost pure stands, but is more often associated with other shrublets such as *Placopoda virgata*, *Justicia rigida*, *Lycium sokotranum*, *Grewia erythraea*, *Ballochia amoena*, *Trichocalyx orbiculatus*, *Dirichletia obovata*, *Asparagus africanus* var. *microcarpus*; some succulents, such as *Aloe perryi* and *Caralluma socotrana*; herbs, *Aerva lanata*, *Glossonema revoilii*, *Cucumis ficifolius*, *Pedalium murex*, *Anagallis arvensis*, with the grass carpet formed mainly by *Aristida adscensionis* and *Melanocenchris abyssinica* (Pl. **56**, fig. 8).

This shrub zone is fairly wide, extending to the river basins and the gravelly foothills, where it merges into the mixed woodlands on the lower slopes, or ends at the foot of the limestone cliffs. Its density is evidently governed by the humidity and the edaphic factors, and some of the gravel plains along the coast support little or no vegetation.

The succession of plants leading to the climax formation of *Croton* shrub zone, has been observed at Ras Karma airfield and other parts of Socotra, where parts of the bush were cleared for runways and roads. The first invaders were the ephemeral and annual herbs dominated by *Tephrosia apollinea*, followed by such perennials as *Corchorus depressus* and *Cucumis prophetarum*, then by perennial prostrate grass, *Panicum rigidum*, as a sand-binder for small mounts of drifting sand, then bushes of *Indigofera* sp.nov. and last of all *Croton socotranus*. The succession has been slow due to predation by goats and sheep and the climax has far from re-established itself in the eight years since the abandonment of the station at Ras Karma.

The vegetation communities and zones described above can safely be attributed to the Subdesert shrub and grass type of Pichi-Sermolli, although the dominant *Croton*-short grass community is not found on the East African mainland.

Minor hills and dry hill slopes

The *Croton socotranus* association frequently encroaches on the hill-sides and sometimes remains dominant there. In some localities, however, particularly at a height of 100–250 m. it becomes at least partly replaced by the *Commiphora* community represented by such xerophilous elements as *Commiphora parvifolia*, *C. socotrana*, *Aloe perryi*, *Euphorbia nubica*, *E. spiralis*, *Barleria tetracantha*, *Blepharis spiculifolia*, *Cissus subaphylla* and others.

It is easier to regard this community as a transition between the subdesert shrub and grass and the subdesert shrub with trees, rather than to attempt to ascribe it to either.

(2) *The limestone plateau*

The slopes of the limestone plateau are often sheer cliffs, but sometimes they are less steep, composed of tumbled-down slabs and chunks of rock and shelves separated by stony screes. Not only is the whole limestone block honeycombed with fissures, caves and ledges, but the individual rocks are scoured with cracks and hollows, where particles of soil accumulate, affording foothold for vegetation (Pl. **57**, fig. 11).

These slopes are veritable rock gardens, surprising for the variety of their flora. There is undoubtedly some gradation with altitude, but the limits were not rigid, particularly for some species; the decisive factor probably being the occurrence of mists, and the main change becomes apparent at about 500 m. The plants growing nearest the edge of the sea have already been mentioned. A short distance above, *Dendrosicyos socotrana*, *Cissus subaphylla*, *Euphorbia arbuscula* and *Adenium sokotranum* combine to form a landscape peculiar to Socotra (Pl. **57**, fig. 9), together with some *Euphorbia nubica*, *E. spiralis*, *Commicarpus* sp., *Maerua socotrana*, *Withania riebeckii*, *Cynanchum linifolum*. In addition, the *Croton socotranus* community becomes established wherever soil deposits are sufficient to permit its development.

The annual and perennial herbs are equally varied and abundant, and the commonest recorded were *Trichodesma microcalyx*, *Pulicaria stephanocarpa*, *P. diversifolia*, *Corchorus erodioides*, *Lactuca rhynchocarpa*, *Crotalaria leptocarpa*, *Ipomoea blepharocephala*, *Boerhavia repens*, *Medicago minima*, *Convolvulus glomeratus*, *Oldenlandia pulvinata*, and the ferns *Actiniopteris australis* and *Adiantum balfourii*.

At the height of 500 m. and above, rock-plants are represented by *Dorstenia gigas*, *Kleinia scottii*, *Ficus socotrana*, *Boswellia* sp., presenting an equally characteristic if somewhat different appearance (Pl. **57**, fig. 10). Other common elements within this mixed community are *Boswellia* sp., *Tetragonia pentandra*, *Adenium socotranum*, *Euphorbia oblanceolata*, *Hibiscus scottii* and some others (Pl. **57**, fig. 11). The young seedlings usually require a small quantity of soil but, once established, the plants appear to draw sustenance from the bare rock.

Other plants, such as *Pseudomussaenda capsulifera*, *Polycarpaea spicata*, *P. divaricata* and *Haya obovata* grow suspended from ledges of rock. Yet others are only found growing in pockets of dark rich soil, deep in the crevices of rocks; of these *Begonia socotrana*, *Exacum affine*, *Peucedanum cordatum* and the fern *Adiantum balfourii* are the commonest. A greater number, however, show preference for screes, shelves and valleys, where some soil becomes accumulated. Where soil deposits are poor, the vegetation is characterized by succulents such as *Aloe perryi*, *Kalanchoe farinacea*, *K. robusta* and some small woody herbs—*Melhania muricata*, *Diceratella incana*, *Leucas urticifolia*, *Helichrysum gracilipes*, *Teucrium sokotranum*, in addition to the above-mentioned rock plants and an occasional *Euphorbia arbuscula*. In sheltered valleys, where soil deposits are more abundant, sometimes fairly dense thickets become established; here the commonest shrubs and trees are represented by *Ruellia insignis*, *Ormocarpum caeruleum*, *Acacia pennivenia*, *Dicliptera effusa*, *Croton sulcifructus*, *Psiadia schweinfurthii*, *Vernonia cockburniana*, *Rhus thyrsiflora*, *Ficus socotrana*, *Justicia heterocarpa*, *Acridocarpus socotranus* and *Cissus quadrangularis*. These are bound by lianas and creepers, such as *C. paniculata*, *Tragia balfouriana*, *Curroria decidua* subsp. *volubilis* and *Dioscorea lanata*.

The above description is based on the vegetation of Reiged, the 900 m. high limestone bluff west of Hadibo. Although the majority of the plants mentioned were also found in the other parts of the limestone plateau, the composition of the vegetation varied and the dominants in one locality were sometimes rare or absent in others. The most noteworthy example is the *Dracaena–Boswellia* community on the slopes of the Hamadera hills at Homhil (Pl. 57, fig. 12), chiefly composed of *Dracaena cinnabari*, *Boswellia ameero*, *B. elongata*, *B. socotrana*, *Aloe perryi*, *Adenium sokotranum* and *Mitolepis intricata*. While *Dracaena* is more common on the limestone slopes, *Boswellia* predominates on the plain

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Figs. 9–12. Explanation of Plate on p. 720.

(Facing p. 712)

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Figs. 13–16. Explanation of Plate on p. 720.

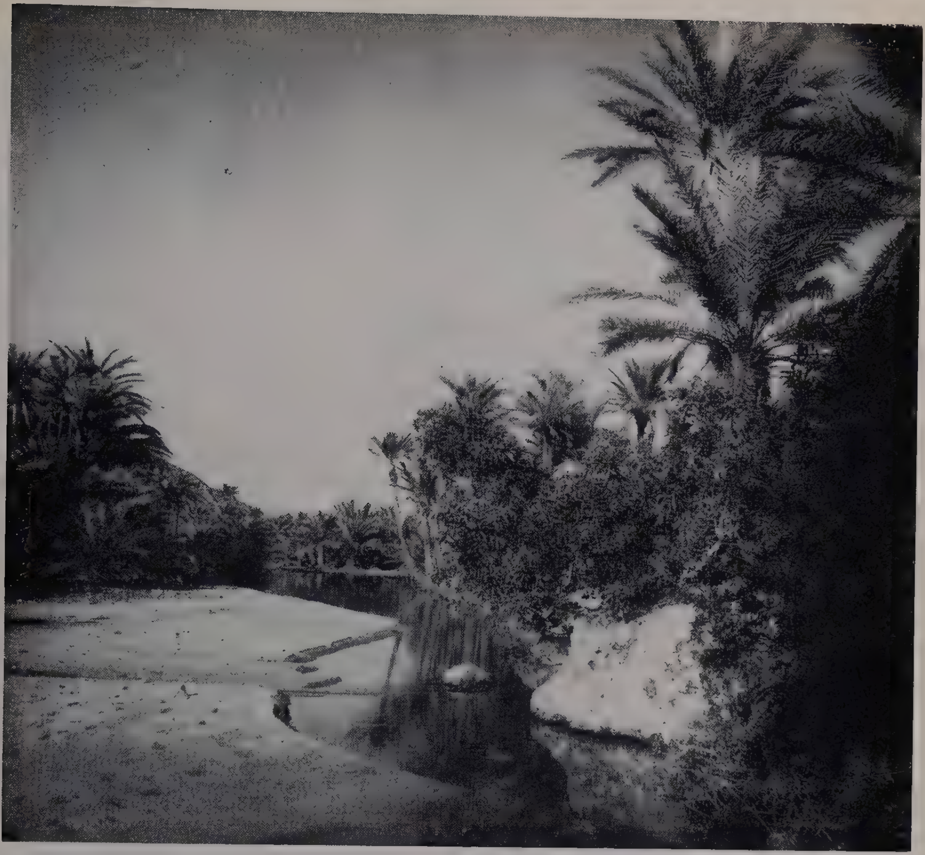

Fig. 17

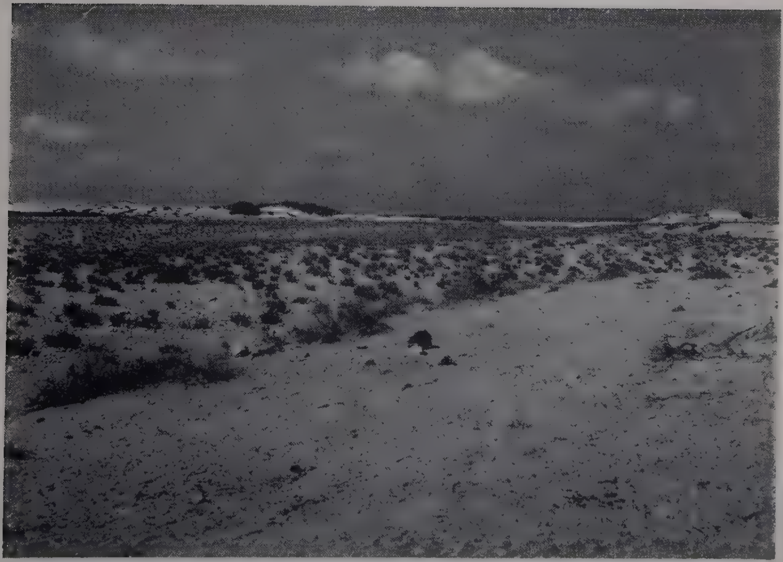

Fig. 18

Explanation of Plate on p. 720.

where, in addition, a species of *Lannea*, not seen elsewhere, forms a small shady grove. The vegetation on the southern hills surrounding Homhil is rather different, forming a mixed shrub thicket, the main components of which are *Rhus thyrsiflora*, *Dirichletia venulosa* and *Punica protopunica*.

Lannea aspleniifolia is a common member of the communities on the limestone slopes inland from Kalansiya, but rare elsewhere, while the vegetation of the cliffs along the southern coastal plain is characterized by a predominance of rock plants, chiefly shrubs, such as *Boswellia* spp., *Dyerophytum pendulum*, *Cryptolapis orbicularis*, *Cochlanthus socotranus*, *Secamone socotrana*, *Euphorbia oblanceolata*, *E. nubica*, *Hibiscus scottii*, *Barleria spinosa* and *Dorstenia gigas*.

The altitudinal zonation is also variable; for example, along the northern coast, *Dorstenia gigas* is seldom seen below 500 m., while along the southern coast it is commonly encountered down to 100 m.

With the exception of the thickets found in the sheltered valleys, the communities of the limestone plateau described so far can be ascribed to the subdesert shrub with trees as has been done by Pichi-Sermolli. The mixed thickets of this region, together with those on the lower slopes of the Hagghier, on the other hand,.may be referred to the subdesert bush and thicket (type 6 of Pichi-Sermolli).

By contrast with the slopes, the top of the main limestone plateau is remarkably arid. The perennial vegetation is rather scanty, consisting of stunted bushes of *Jatropha unicostata*, *Croton socotranus*, *Ficus socotrana*, *Adenium sokotranum*, *Aloe perryi* and an occasional *Dracaena cinnabari*. The annual vegetation is more abundant, being chiefly composed of grasses—*Hyparrhenia hirta*, *Arthraxon lancifolius*, *Aristida funiculata*, *Cymbopogon* sp. and *Pennisetum setaceum*; some herbs—*Asphodelus tenuifolius*, *Digera alternifolia*, *Achyranthes aspera* and some others (Pl. **58**, fig. 13).

Here again there is some difference in the plant composition between the various parts of the island: thus the community populating the summit of the Hamadera hill is chiefly characterized by low woody perennials such as *Mitolepis intricata*, the larger shrubs and trees being absent. The watershed between the coastal valley of Kalansiya and the Goba plain supports a thin growth of *Jatropha unicostata* and *Adenium sokotranum*, in parts replaced by the *Croton* association.

The paucity of the vegetation on the plateau may not be so much due to the soil and aridity, since many vegetation communities develop well on rocky slopes under even more arid conditions, as to the high winds, particularly during the south-west monsoon. It is significant that vegetation was found to be much better developed in ravines and gorges where the adjoining cliffs afford some protection. Thus on Reiged, mixed thickets have developed on the uppermost shelf, but are absent from the summit.

Parts of the limestone plateau are indeed so sparsely clothed with vegetation that one feels tempted to ascribe them to the desert vegetation, as has been done by Pichi-Sermolli on the information provided by Balfour (1888). However, the sparsity of the vegetation here is mainly due to one outstanding climatic factor (wind) and not general desert conditions, and many of the species found here are prominent members of the semi-arid vegetation elsewhere on Socotra. In all fairness, therefore, one should refer the largest part of the limestone plateau to the Subdesert shrub and grass type of Pichi-Sermolli, with islands of less arid vegetation belonging to the Subdesert shrub with trees and the Subdesert bush and thicket types.

(3) *The granite massif of the Hagghier*

Along the northern slopes, the coastal shrub-zone extends to the foothills, where it merges with the mixed thickets composed of a variety of shrubs such as *Jatropha unicostata*, *Dirichletia obovata*, *Cordia obovata*, *Cylista* sp., *Acridocarpus socotranus*; trees like *Sterculia rivae*, *Aberia abyssinica* and *Tamarindus indica*, and an undergrowth of herbs and annuals such as *Teucrium balfourii*, *Leucas neuflizeana*, *L. urticifolia*, *L. virgata*, *Justicia heterocarpa* and many others mentioned for the shrub zone and the lower slopes of limestone plateau (Pl. 58, fig. 14).

With an increase in altitude, and presumably rainfall, vegetation becomes denser; many of the elements mentioned for the higher slopes of the limestone plateau such as *Ruellia insignis*, *Rhus thyrsiflora*, *Ormocarpum caeruleum*, *Clerodendrum galeatum* are also fairly common here, but some due to better edaphic conditions present a somewhat different aspect. Thus, *Ficus socotrana*, which in the limestone belt grows as a stunted rock shrub, here develops into a fine spreading tree.

There is no difficulty in ascribing these mixed thickets together with those of the sheltered valleys of the limestone region to the subdesert bush and thicket type of Piçhi-Sermolli. These thickets gradually change to the evergreen thickets of the Hagghier Highlands, which belong to the semi-arid vegetation zone.

The main change in vegetation becomes apparent at an altitude of over 750 m., where many elements appear for the first time. The vegetation of the Hagghier Highlands may be divided into three main types: the grasslands, the thickets and the association of woody herbs. One might include the rock vegetation, but this community does not reach the same development on granites, as on the limestone. The surface of rocks is covered with lichens so thickly that the naturally pink granite appears grey from a distance. The higher forms of flora, however, are restricted to the occasional fissures where succulents such as *Kalanchoe farinacea*, *K. rotundifolia*, *Aloe perryi*, and some herbs such as *Exacum affine*, *E. caeruleum* and *Begonia socotrana* find a foothold. However, there appear to be no rock shrubs.

The grasslands are to a large extent composed of *Themeda quadrivalvis*, *Hyparrhenia hirta* and *Arthraxon lancifolius* (Pl. 58, fig. 15). They form the main pastures for the Socotran cattle and cover a fairly large area of the watershed between the granite peaks. The division between the grasslands and the thickets is a very sharp one.

The thickets occupy the lower slopes of the highlands, but are absent from the steeper peaks. Their specific composition is a rich and varied one, the following being the commonest in order of their dominance: shrubs and small trees—*Cephalocroton socotranus*, *Carissa edulis*, *Buxus hildebrandtii*, *Dodonaea viscosa*, *Ficus socotrana*, *Indigofera sokotrana*, *Ruellia insignis*, *Boswellia ameero* and *Euphorbia socotrana*; smaller bushes—*Hedyotis stellarioides*, *Hypoestes pubescens*, *Allophylus rhusiphyllus*, together with a tangled undergrowth of *Cocculus balfourii*, *Cissus quadrangularis*, the twining *Tragia balfouriana* and *Ectadiopsis* sp. and the *Dioscorea lanata* lianas (Pl. 58, fig. 16).

The community of the woody herbs develops on the stony slopes leading steeply from the watershed, where it replaces the grasslands and the thickets. This is characterized by such species as *Euryops socotranus*, *Hypericum tortuosum*, *H. mysorense* and *Aerva revoluta*, with an almost Alpine appearance. Other common perennial and annual herbs include *Pluchea obovata*, *P. aromatica*, *Pulicaria vieraeoides*, *Gnidia socotrana*, *Gaillonia puberula*, *Satureja remota*, *Sigesbeckia orientalis* and *Lotus ononopsis*.

Dracaena cinnabari is fairly common, though never as dominant as at Homhil; the other plants noticeable for their appearance being the flat-topped *Commiphora planifrons* and large-leaved amaryllid, *Haemanthus grandifolius*.

The higher peaks of the Hagghier, above 1200 m., were not visited, but according to the earlier descriptions, they are characterized by such woody herbs as *Nirarathamnos asarifolius*, *Dichrocephala chrysanthemifolia* and various species of *Helichrysum*.

The vegetation of the Hagghier Highlands belongs to the semi-arid zone, and one can attribute the *Themeda–Hyparrhenia* grassland to the Open grassland and the thickets to the Evergreen scrub (types 3 and 4) of Pichi-Sermolli. The nanophanerophytic community of the Hagghier is less easy to classify. Climatically it belongs here, physiognomically to the Subdesert shrub and grass type of the arid zone. Perhaps it is best to regard it as part of the Evergreen scrub type.

The southern slopes of the Hagghier are more arid than the northern, particularly at lower altitudes, where mixed thickets soon become replaced by the *Croton* shrub, or *Boswellia*—succulent communities, which in the southern part of Socotra extend to a greater altitude than in the northern. *Aloe forbesii*, in this area, almost completely replaces *A. perryi.*

(4) *Riverine communities*

The majority of the streams on Socotra are sporadic, carrying water only during and for a short time after rains. In their upper reaches, particularly, the vegetation fringing these runnels is hardly different from that of the adjoining slopes. There are, however, a number of springs, streams and pools and some river estuaries, which retain water for a greater part of the year and thus encourage the formation of plant communities not represented, or at least not so fully developed elsewhere. The following are the most noteworthy.

(*a*) The semi-aquatic community represented by *Juncus arabicus* consociation, which forms along most estuaries, as well as along some of the stagnant pools and springs in the interior, where in addition it includes the tall sedge *Cladium mariscus.*

The shallower parts and edges of sluggish streams are lined with *Lythrum hyssopifolia*, *Phyla nodiflora* and with the aquatic grass, *Paspalidium geminatum*, growing in deeper water. In sheltered parts along the edge of streams, ferns such as *Pteris vittata* and *Adiantum balfourii* are common. The upper parts of estuaries, where water begins to stagnate, are carpeted with a low spongy growth of sedges and grasses of the genera *Fimbristylis*, *Cyperus*, *Eragrostis* and *Paspalidium.*

(*b*) The date palm, *Phoenix dactylifera*, which is the main cultivated plant on the island, is planted along the streams, where water-table was high and wherever soil permits this. In addition, the streams with the water at or near the surface are lined with groves of *Ficus salicifolia*, *Euclea* sp., *Cordia obtusa*, *Acridocarpus socotranus*, and *Buxus hildebrandtii* with an occasional larger tree such as *Sterculia rivae*, *Lannea ornifolia*, *Tamarindus indica* and *Ziziphus* sp., the latter usually associated with drier conditions. There are also many herbs, particularly common along these watercourses: *Leucas virgata*, *Ocimum hadiense*, *Hypoestes sokotrana*, *Cassia tora*, *Heliotropium zeylanicum*, *Hibiscus sidiformis*, *Aerva javanica*, *Pedalium murex* and *Vernonia cinerascens* being the most prominent, while the ephemeral grasses are represented by *Aristida adscensionis*, *Chloris barbata*, *Cenchrus setigerus*, *Rhynchelytrum microstachyum*, *Apluda mutica* and *Heteropogon contortus* (Pl. **59**, fig. 17).

(*c*) The drier, sandy stretches of main watercourses, where surface water is absent most of the year, such as the one at Houlaf, are characterized by *Ziziphus* sp., *Ochradenus baccatus*, and such herbs as *Aerva javanica*, *Tephrosia apollinea*, *Cleome* sp. and *Ruta graveolens.*

The above description is based on the Hadibo plain, but is generally true of the northern coast as a whole. The valleys of the southward draining rivers, which cross the Naukad plain, were found to be larger and more arid and the change of the vegetation more gradual. The southern riverine valleys of the Hagghier contain groves of the wild orange *Citrus aurantium*, *Acridocarpus socotranus*, *Peperomia reflexa*, *Ziziphus* sp. and *Tamarindus* trees together with an occasional *Borassus* palm. The lower reaches support *Ziziphus* sp. and the much-branching smaller *Ziziphus* sp., the latter persisting all the way to the coastal plain, where the sandy dry bed of rivers is, in addition, dotted with bushes of *Aerva microphylla*, *Indigofera* sp.nov. and *Dactyloctenium hackelii* much more densely than the adjoining plain (Pl. **59**, fig. 18).

(5) *Agriculture*

Most of the flood waters quickly drain off Socotra, but a small quantity becomes absorbed and later reappears as small streams and springs. The granite range is particularly water-bearing and many streams draining from this range are said to flow for about eight months in a year, while permanent springs abound in this region. The limestone plateau is much more arid, particularly at the western end of the island, but even here there are a number of permanent springs, while small amounts of rain water, which collect in hollows, may suffice for human consumption for up to 3 months after rain.

On the southern coast, water is scarce, limited to one or two springs at the base of cliffs and several wells of brackish water. On the northern coast, the estuaries of larger rivers retain water for most of the year and water-table is high at Hadibo, Ghadheb and Kalansiya, where nearly every household has its well. On the Goba plain, however, water is brackish.

Agriculture is practised on a small scale. Date gardens exist along most estuaries and river basins on the north coast, while on the southern, there is an extensive plantation at Mahallas. Where soil is inadequate for the growth of the plant, additional soil is piled up against the roots, within a circular stone wall, giving the palms the appearance of growing in pots.

Vegetable gardens, irrigated from wells, exist at Hadibo and one or two other villages along the north coast. Sweet potatoes, pumpkins, cotton, tomatoes, pepper and some other vegetables are grown for household use.

There are also one or two small fields of finger millet (*Eleusine coracana*) at Moabbadh, irrigated from the adjoining stream. These are said to be the property of the Sultan and are probably still in the experimental stage.

Wild orange trees (*Citrus aurantium*) are found in abundance in the valleys of the southern Hagghier. The plant may have been originally introduced, but appears to be growing wild now. The pods of *Tamarindus indica*, the berries of *Cordia* sp. and some other indigenous plants such as *Glossonema revoilii* (fruit) and *Dioscorea lanata* (tubers) are eaten.

Although most of the population of Socotra is pastoral, and stock breeding is undertaken as keenly as on the adjoining Somaliland Peninsula, overgrazing does not seem to be a problem on Socotra. This is almost certainly due to a balance of stock population maintained by natural causes in the absence of veterinary services, rather than to any control by the inhabitants. In any case, the recent census shows no notable increase in either human or stock population since the end of the last century, or even compared with the figures given by early travellers.

(6) *Weeds of cultivations*

Many of the weeds have probably been introduced relatively recently, as suggested by their abundance in the cultivations in the vicinity of villages and their relative rarity elsewhere. The commonest noted were *Argemone mexicana*, *Portulaca oleracea*, *Aizoon canariense*, *Trianthema pentandra*, *Psoralea corylifolia*, *Datura metel*, *Solanum coagulans*, *Cassia tora*, *Cassia* sp., *Ricinus communis* and some others. These are common both in the palm-gardens and the small vegetable gardens near the villages. Other weeds are often also common members of the coastal and some other communities on the island, and a few of them are endemic to Socotra. Of these, *Heliotropium dentatum*, *Zygophyllum simplex*, *Achyranthes aspera*, *Digera alternifolia*, *Indigofera tinctoria* and *Sida ovata* are the most noteworthy.

SUMMARY

Our information on the extent and the distribution of the vegetation types on Socotra referable to the arid zone may be summarized as follows:

1. *Maritime vegetation* is present over small areas along the coast of Socotra. The observed communities have been described and similar, or slightly different, ones are believed to exist to a limited extent in other parts of the island which were not seen, such as near Kalansiya and at Shoab and possibly elsewhere.

2. *Desert vegetation.* No vegetation community can truly be ascribed to this type. There are limited gravel and sand stretches on the coastal plain, where the paucity of the vegetation is due to edaphic aridity, and parts of the limestone plateau, where perennial growth is reduced by winds, but the existing vegetation can be described as a debased form of other plant communities reaching the climax under more favourable conditions.

3. *Subdesert shrub and grass* covers most of the island, i.e. the whole of the southern coast, most of the northern coast and the western and central parts of the limestone plateau.

4. *Subdesert shrub with trees* is another well-represented vegetation type, comprising the rock communities of the limestone slopes, the *Boswellia–Dracaena* community of Homhil and possibly other similarly sheltered parts of the limestone plateau.

5. *Subdesert scrub* is not represented, at least in its typical composition. On the basis of the vegetation cover one might possibly regard the denser *Croton* formations as belonging to this type, but this would be atypical in relation to the communities characteristic of this type.

6. *Subdesert bush and thicket.* The mixed thickets of the lower slopes of the Hagghier and some of the sheltered valleys within the limestone region, such as the Goahal gorge can only be ascribed to this type, even though somewhat atypical.

7. *Xerophilous open woodland* is not represented in its typical composition.

8. *Vegetation of sites where water is present* includes numerous riverine communities and the cultivations of Socotra.

9. *Vegetation of semi-arid type.* The vegetation of the semi-arid zone is confined to the highlands of the Hagghier, above the height of 850 m., where only two vegetation types can be recognized, the Open grassland and the Evergreen scrub.

Species referred to in G. B. Popov's paper, 'The Vegetation of Socotra'

by J. B. Gillett, Royal Botanic Gardens, Kew.

Families in the sequence of Bentham and Hooker, *Genera Plantarum*

Taxa marked with an asterisk are believed to be endemic to Socotra, those with two asterisks belong to genera endemic to Socotra (in view of our imperfect botanical knowledge of the Horn of Africa these statements must be considered as provisional).

- Menispermaceae
  - **Cocculus balfourii* Schweinf. ex Balf. f.
- Papaveraceae
  - *Argemone mexicana* P.
- Cruciferae
  - **Diceratella incana* Balf. f.
  - *Farsetia longisiliqua* Decne.
- Capparidaceae
  - *Cadaba rotundifolia* Forsk.
  - *Cleome* sp.
  - *Maerua socotrana* (Schweinf.) Gilg
- Resedaceae
  - *Ochradenus baccatus* Del.
- Flacourtiaceae
  - *Aberia abyssinica* Clos
- Caryophyllaceae
  - ***Haya obovata* Balf. r.
  - **Polycarpaea divaricata* Balf. f.
  - *P. spicata* Wight ex Arn.
- Portulacaceae
  - *Portulaca oleracea* L.
  - *P. quadrifida* L.
- Tamaricaceae
  - *Tamarix sokotrana* Vierh.
- Hypericaceae
  - *Hypericum mysorense* Wight & Arn.
  - **H. tortuosum* Balf. f.
- Malvaceae
  - **Hibiscus scottii* Balf. f.
  - *H. sidiformis* Baill. (*H. ternatus* (Cav.) Mast. not of Cav.)
  - *Sida ovata* Forsk.
- Sterculiaceae
  - *Melhania muricata* Balf. f.
  - *Sterculia rivae* (K. Schum.) Chiov.
- Tiliaceae
  - *Corchorus depressus* (L.) Chistens.
  - **C. erodioides* Balf. f.
  - *Grewia erythraea* Schweinf.
- Malpighiaceae
  - **Acridocarpus socotranus* Oliv.
- Zygophyllaceae
  - **Fagonia paulayana* Wagn. & Vierh. ex Vierh.
  - *F. socotrana* (Balf. f.) Schweinf.

Zygophyllaceae (_cont._)
Tribulus terrestris L.
Zygophyllum simplex L.
Rutaceae
Ruta graveolens L.
Citrus aurantium L.
Burseraceae
*_Boswellia ameero_ Balf. f.
*_B. elongata_ Balf. f.
*_B. socotrana_ Balf. f.
Commiphora parvifolia (Balf. f.) Engl.
*_C. planifrons_ (Balf. f.) Engl.
*_C. socotrana_ (Balf. f.) Engl.
Rhamnaceae
Zizyphus sp.
Vitaceae
*_Cissus paniculata_ (Balf. f.) Planch.
C. quandrangularis L.
*_C. subaphylla_ (Balf. f.) Planch.
Sapindaceae
Dodonaea viscosa (L.) Jacq.
*_Allophylus rhusiphyllus_ Balf. f.
Anacardiaceae
*_Lannea aspleniifolia_ (Balf. f.) Engl.
*_L. ornifolia_ (Balf. f.) Engl.
*_Rhus thyrsiflora_ Balf. f.
Leguminosae: Papilionatae
Crotalaria leptocarpa Balf. f.
Cylista sp.
Indigofera colutea (Burm. f.) Merr.
I. cordifolia Heyne ex Roth
I. nephrocarpa Balf. f.
I. oblongifolia Forsk.
*_I. sokotrana_ Vierh.
I. tinctoria L.
*_Lotus ononopsis_ Balf. f.
Medicago mimima L.
Ormocarpum caeruleum Balf. f.
Psoralea corylifolia L.
Tephrosia apollinea (Del.) Link.
Caesalpinioideae
Cassia tora L.
Tamarindus indica L.
Mimosoideae
Acacia edgeworthii T. Anders. (_A. socotrana_ Balf. f.)
*_A. pennivenia_ Balf. f.
Crassulaceae
*_Kalanchoe farinacea_ Balf. f.
*_K. robusta_ Balf. f.
K. rotundifolia Haw.
Lythraceae
Lythrum hyssopifolia L.
Punicaceae
*_Punica protopunica_ Balf. f.
Cucurbitaceae
Cucumis ficifolius A. Rich.
C. prophetarum L.
**_Dendrosicyos socotrana_ Balf. f.
Begoniaceae
*_Begonia socotrana_ Hook. f.
Aizoaceae
Aizoon canariense L.
*_Tetragonia pentandra_ Balf. f.
Trianthema pentandra L.
Umbelliferae
**_Nirarathamnos asarifolius_ Balf. f.
*_Peucedanum cordatum_ Balf. f.
Rubiaceae
Dirichletia obovata Balf. f.
*_D. venulosa_ Balf. f.
*_Gaillonia puberula_ Balf. f.
*_Hedyotis stellarioides_ Balf. f.
*_Oldenlandia pulvinata_ (Balf. f.) Vierh.
**_Placopoda virgata_ Balf. f.
*_Pseudomussaenda capsulifera_ (Balf. f.) Wernham
Compositae
Ageratum conyzoides L.
Bidens biternata (Lour.) Merril & Sherff
Dichrocephala chrysanthemifolia (Bl.) DC.
*_Euryops socotranus_ Balf. f.
Helichrysum gracilipes Oliv. & Hiern.
*_Kleinia scottii_ (Balf. f.) Chiov.
*_Lactuca rhynochocarpa_ Balf. f.
*_Pluchea aromatica_ Balf. f.
*_P. obovata_ Balf. f.
*_Psiadia schweinfurthii_ Balf. f.
*_Pulicaria diversifolia_ Balf. f.
*_P. stephanocarpa_ Balf. f.
*_P. vieraeoides_ Balf. f.
Sigesbeckia orientalis L.
Vernonia cinerascens Sch. Bip.
*_V. cockburniana_ Balf. f.
Plumbaginaceae
*_Dyerophytum pendulum_ (Balf. f.) Kuntze
Limonium sp.
Primulaceae
Anagallis arvensis L.
Salvadoraceae
Salvadora persica L.
Ebenaceae
Euclea sp.
Apocynaceae
*_Adenium sokotranum_ Vierh.
Carissa edulis (Forsk.) Vahl
Asclepiadaceae
Calotropis procera (Ait.) Ait. f.
Caralluma socotrana (Balf. f.) N.E. Br.
**_Cochlanthus socotranus_ Balf. f.
Cryptolepis orbicularis Chiov.
Curroria decidua Planch. ex Benth. ssp. _volubilis_ (Balf. f.) Bullock
*_Cynanchum linifolium_ (Balf. f.) Bullock comb.nov. (_Vincetoxicum linifolium_ Balf. f. in _Proc. R. Soc. Edinb._ **12**, 79 (1884))
Ectadiopsis sp. (sensu Balf. f.)
Glossonema revoilii Franch.

*******Mitolepis intricata* Balf. f.
**Secamone socotrana* Balf. f.
Gentianacea
**Exacum affine* Balf. f.
**E. caeruleum* Balf. f.
Boraginaceae
Arnebia hispidissima (Lehm.) DC.
**Cordia obovata* Balf. f.
**C. obtusa* Balf. f.
**Heliotropium dentatum* Balf. f.
H. zeylanicum (Burm. f.) Lam.
**Trichodesma microcalyx* Balf. f.
Convolvulaceae
Convolvulus fastigiatus Roxb.
C. glomeratus Choisy
Ipomoea blepharosepala Hochst. ex A. Rich.
I. pescaprae (L.) Roth
Seddera latifolia Hochst. & Steud. ex Hochst.
Solanaceae
Datura metel L.
**Lycium sokotranum* Wagn. & Vierh.
Solanum coagulans Forsk.
**Withania riebeckii* Schweinf. ex Balf. f.
Scrophulariaceae
**Campylanthus spinosus* Balf. f.
**Lindenbergia sokotrana* Vierh.
Pedaliaceae
Pedalium murex L.
Acanthaceae
***Ballochia amoena* Balf. f.
Barleria spinosa Hook. ex Nees
**B. tetracantha* Balf. f.
**Blepharis spiculifolia* Balf. f.
**Dicliptera effusa* Balf. f.
**Hypoestes pubescens* Balf. f.
**H. sokotrana* Vierh.
Justicia heterocarpa T. Anders.
**J. rigida* Balf. f.
**Ruellia insignis* Balf. f.
**Trichocalyx orbiculatus* Balf. f.
Verbenaceae
Avicennia marina (Forsk.) Vierh.
**Clerodendrum galeatum* Balf. f.
Phyla nodiflora (L.) Greene
Labiatae
Leucas neuflizeana Courb.
L. urticifolia (Vahl) Benth.
**L. virgata* Balf. f.
Ocimum hadiense Forsk.
**Satureja remota* (Balf. f.) Vierh.
**Teucrium balfourii* Vierh.
**T. sokotranum* Vierh.
Nyctaginaceae
Boerhavia repens L.
Commicarpus sp.
Amaranthaceae
Achyranthes apsera L.
Aerva javanica (Burm. f.) Juss. ex Schult.
A. lanata (L.) Juss. ex Schult.
A. microphylla Moq.
**A. revoluta* Balf. f.
Digera alternifolia (L.) Aschers.
Chenopodiaceae
Arthocnemum sp.
Atriplex stocksii Boiss. forma *sokotrana* (Vierh.) Vierh.
Salsola forskalii Schweinf.
Suaeda monoica Forsk.
Thymedleaceae
**Gnidia socotrana* (Balf. f.) Gilg
Buxaceae
Buxus hildebrandtii Baill.
Euphorbiaceae
**Cephalocroton socotranus* Balf. f.
**Croton socrotranus* Balf. f.
**C. sulcifructus* Balf. f.
**Euphorbia arbuscula* Balf. f.
E. nubica N.E. Br.
**E. oblanceolata* Balf. f.
**E. septemsulcata* Vierh.
**E. socotrana* Balf. f.
**E. spiralis* Balf. f.
**Jatropha unicostata* Balf. f.
Phyllanthus sp.
Ricinus communis L.
Tragia balfouriana* Gillett nom.nov. (*T. dioica* Balf. f., *Proc. R. Soc. Edinb.* **12, 95 (1884), non Sond., *Linnaea* **23**, 109 (1850))
Moraceae
**Dorstenia gigas* Schweinf. ex Balf. f.
Ficus salicifolia Vahl
**F. socotrana* Balf. f.
Amaryllidaceae
**Haemanthus grandifolius* Balf. f.
Dioscoreaceae
**Dioscorea lanata* Balf. f.
Liliaceae
**Aloe forbesii* Balf. f.
**A. perryi* Bak.
**Asparagus africanus* Lam. var. *microcarpus* Balf. f.
Asphodelus tenuifolius Cav.
**Dracaena cinnabari* Balf. f.
Juncaceae
Juncus arabicus (Asch. & Buch.) Adamson
Palmae
Borassus sp.
Phoenix dactylifera L.
Cyperaceae
Cladium mariscus R. Br.
Cyperus sp.
Fimbristylis sp.
Gramineae
Aeluropus sp.
Apluda mutica L.
Aristida adscensionis L.
A. funiculata Trin. & Rupr.
Arthraxon lancifolius (Trin.) Hochst.

Gramineae (*cont.*)
- *Cenchrus ciliaris* L.
- *C. setigerus* Vahl
- *Chloris barbata* Sw.
- *Cymbopogon* sp.
- *Dactyloctenium aristatum* Link.
- **D. hackelii* Wagn & Vierh. ex Vierh.
- *Eleusine coracana* (L.) Gaertn.
- *Enneapogon* sp.
- *Eragrostis* sp.
- *Heleochloa dura* Boiss.
- *Heteropogon contortus* (L.) Beauv. ex Roem. & Schult.
- *Hyparrhenia hirta* (L.) Stapf.
- *Melanocenchris abyssinica* (R.Br. ex Fres.) Hochst.
- **Panicum rigidum* Balf. f.
- *Paspalidium geminatum* (Forsk.) Stapf.
- *Pennisetum setaceum* (Forsk.) Chiov.
- **Rhynchelytrum microstachyum* Balf. f.
- *Sporobolus spicatus* (Vahl) Kunth
- *Themeda quadrivalvis* (L. f.) Kuntze

Filices
- *Actiniopteris australis* (L. f.) Lk.
- **Adiantum balfourii* Bak.
- *Pteris vittata* L.

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EXPLANATION OF PLATES 55–59

PLATE 55

Fig. 1. Bare, crescentic dunes overlying stony floor of the southern coastal plain of Naukad. The absence of vegetation is due to edaphic aridity.

Fig. 2. Sand deposits at Houlaf, northern coast. *Acacia edgeworthii* forms a community here, but is rare elsewhere.

Fig. 3. Sward of salt-grass, *Heleochloa dura*, on the beach dunes at Naukad. In the background, the belt of the sea-lavender, *Limonium* spp. which develops farther inland from the salt-grass.

Fig. 4. Sometimes the vegetation on the southern coastal plain is very sparse. Low crescentic dunes with a few shrubs of *Calotropis procera*.

PLATE 56

Fig. 5. At the base of the hills the dunes are fixed by a community of woody herbs and ephemerals.

Fig. 6. *Indigofera* sp.nov.—short grass association on the coastal plain at Hadibo.

Fig. 7. Another woody herb community: the *Dactyloctenium hackelii–Euphorbia spiralis* association on the Goba plain.

Fig. 8. The shrub zone; *Croton socotranus*—short grass association on Hadibo plain and at Moabbadh.

PLATE 57

Fig. 9. Community of rock plants on the lower slopes of the Reiged. (*a*) *Dendrosicyos socotrana*, (*b*) *Cissus subaphylla* and (*c*) *Euphorbia arbuscula*.

Fig. 10. Community of rock plants on the higher slopes of Reiged. (*a*) *Kleinia scottii*, (*b*) *Ficus socotrana*, (*c*) *Dorstenia gigas*, (*d*) *Boswellia* sp.

Fig. 11. Rock vegetation on the middle slopes of the Reiged; the dominants are succulents and shrubs.

Fig. 12. A grove of *Dracaena cinnabari* on the slopes of the Hamadera hill at Homhil.

PLATE 58

Fig. 13. A typical view of the summit of the limestone plateau, with stunted shrubs (*Jatropha unicostata*) and ephemerals.

Fig. 14. Mixed thickets on the lower slopes of the Hagghier.

Fig. 15. Grasslands on the Hagghier mountains; dominants *Themeda quadrivalvis* and *Hyparrhenia hirta*.

Fig. 16. Mixed evergreen thickets in the Hagghier highlands.

PLATE 59

Fig. 17. *Ficus salicifolia*, *Cordia* sp. and other plants which together with the date palm form fairly dense groves along the rivers, which carry water for most of the year.

Fig. 18. Dry watercourse crossing the Naukad plain. Vegetation is denser, but of the same composition as on the adjoining plain.

Variation in the flower of Eugenia malaccensis Linn.

By D. M. A. Jayaweera, M.Sc. (Lond.), F.L.S.,
Superintendent, Royal Botanic Gardens, Peradeniya

(With 7 Text-figures)

[Read 19 January 1956]

The morphology of the flower of *Eugenia malaccensis* Linn., has not hitherto been the subject of detailed study. Mention is, however, made by Worsdell (1916) of certain teratological features in the flower of the Myrtaceae. The results of an investigation made on four trees of *E. malaccensis*, in the Royal Botanic Gardens, Peradeniya, during the period 1951–2, are reported herein.

The normal flower in this species is briefly described below:

Calyx. Sepals four, free, slightly overlapping at the base, persistent in fruit.

Corolla. Petals four, free, valvate or slightly overlapping at the margins, alternating with sepals.

Androecium. Stamens 325–400, more or less at the same level and internal to the corolla, innermost stamens sterile.

Gynaecium. Carpels two, fused, bilocular, inferior, with axile placentation.

RESULTS

Frequency distributions. An examination of over 3500 flowers from the four trees, which bloomed in December 1951 and October 1952, revealed striking and frequent deviations from the normal structure indicated above. The counts are presented in Tables 1 and 2.

Table 1

		No. of petals					
		2	3	4	5	6	Total
No. of sepals	2	—	—	—	—	—	—
	3	—	—	3	—	—	3
	4	—	4	2867	39	2	2912
	5	—	4	28	47	—	79
	6	1	—	—	3	2	6
Total		1	8	2898	89	4	3000

Table 2

		No. of carpels		
		2	3	Total
No. of perianth segments	7	3	4	7
	8	2855	17	2872
	9	60	7	67
	10	41	8	49
	11	1	2	3
	12	2	—	2
Total		2962	38	3000

Of the 3000 flowers included in the counts in Table 1, 2867 had the normal 4-merous structure, forty-seven had a pentamerous perianth, and two were trimerous with six sepals and six petals; the trimerous calyx and corolla were each arranged in two alternating whorls of three members. The correlation between sepal number and petal number is high: $r = +0{\cdot}932 \pm 0{\cdot}0117$.

Table 2 indicates the relation between the frequency of total perianth segments and carpel number. Of a total of 3000 flowers, thirty-eight showed 3-carpellary ovaries. Seven

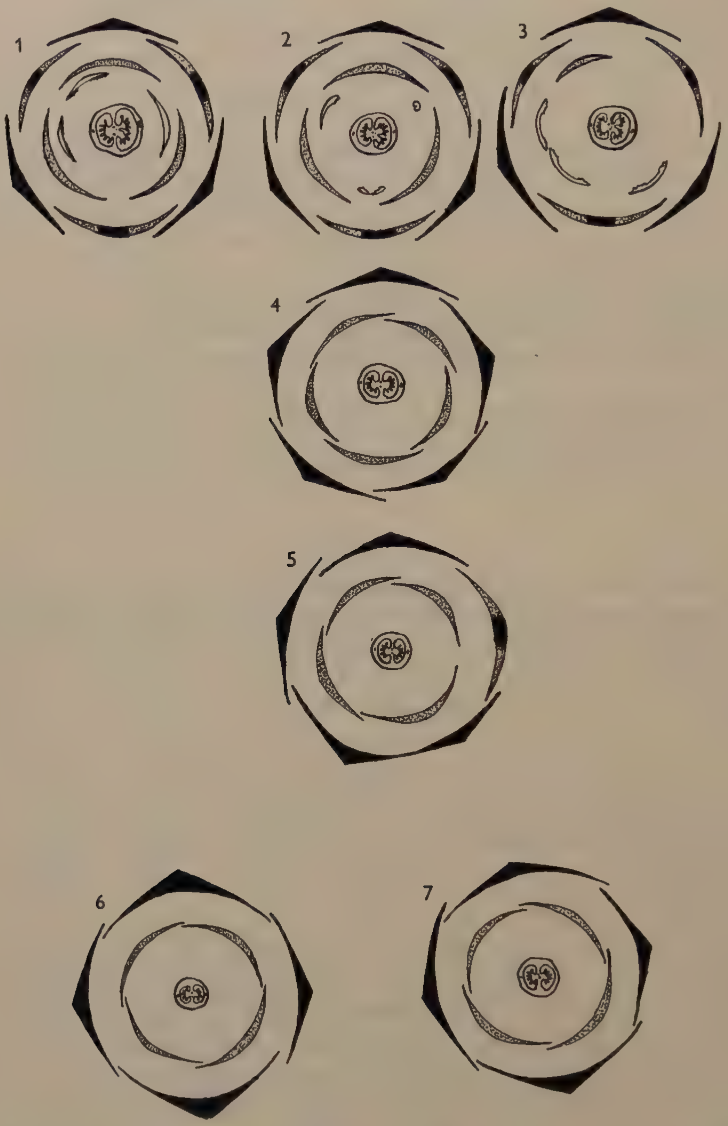

Fig. 1. Floral diagrams of some abnormal flowers showing the trimerous cum pentamerous origin of the perianth. The stamens are omitted for convenience. (1) A typical trimerous flower showing two whorls of perianth segments and two whorls of staminodes; members of each whorl alternating with those of the next. The ovary is bicarpullary but one of the loculi is much larger than the other and presents two placentas inside. (2) Another flower showing the same arrangements as (1) but the innermost whorl of staminodes is more stamen-like. (3) Another flower showing the same arrangement but the two innermost whorls of staminodes is represented by four petaloid segments. (4) A typical pentamerous flower. (5) Diagram showing the fusion of two sepals and the presence of a petaloid sepal in the calyx whorl. (6) Diagram of a typical 4-merous flower with two of its opposite sepals being overlapped by the other two opposite. (7) Four-merous flowers, but one of its sepals is completely outside and the other opposite is being overlapped by the two adjacent to it.

of these flowers were trimerous in respect of both perianth and pistil. The correlation between number of perianth segments and carpel number is low but significant: $r = +0{\cdot}4185 \pm 0{\cdot}0101$.

Teratology. Less than 0·3 % of the flowers were trimerous in both calyx and corolla. The petals were sepaloid and had green centres. One or more whorls of staminodes alternated with petals (Fig. 1 (1–3)). As will be indicated later, some of the staminodes were transitional forms between petals and stamens. One of the two loculi in the ovary was larger than the other and possibly consisted of two carpels; the bilocular ovary would then be tricarpellary.

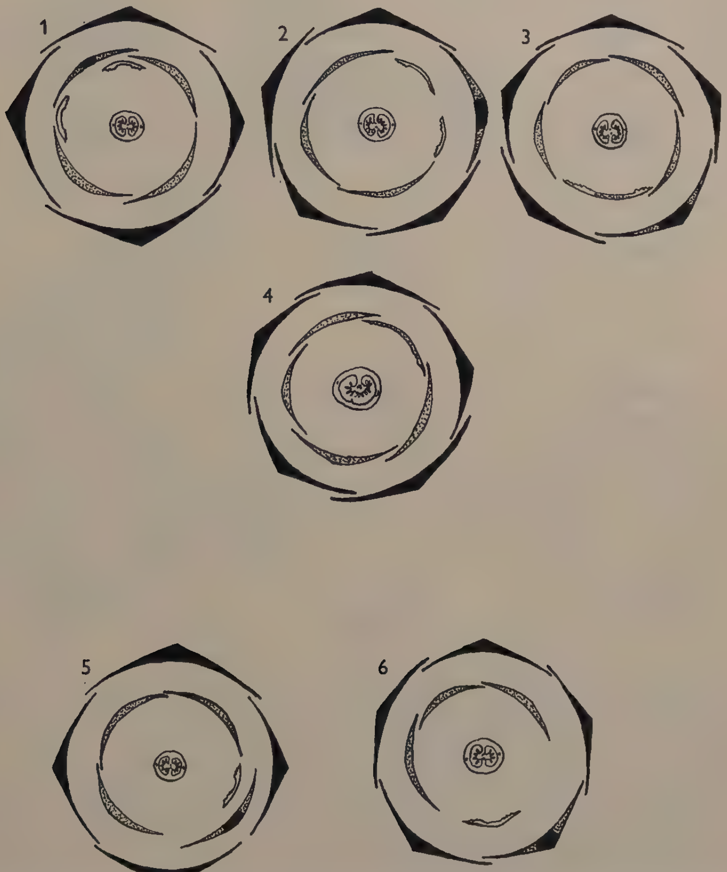

Fig. 2. Floral diagrams of some abnormal flowers showing probable signs of reversion to a pentamerous condition. (1) Diagram showing one of the petals becoming sepaloid and the two staminodes inner to it taking a petal-like form. (2) The sepaloid petal has migrated to the calyx whorl and the two staminodes have occupied the gap left behind by the sepaloid petal. (3) Same as (2) but the staminodes are more petal-like. (4) Same as (3) but the staminodes have lost all traces of their origin and the flower has become typically pentamerous. The ovary is unilocular, one of the septa not having developed. (5) Diagram of a 4-merous flower where the sepaloid petal is half-way between the calyx and corolla whorls and its place being occupied by a single staminode. (6) Same as (5) but migration of the sepaloid petal to the calyx whorl has been completed.

Flowers pentamerous in calyx and corolla were relatively frequent. Both calyx and corolla were always distinctly imbricate and a difference in the size of the two loculi that compose the ovary was observed in few instances. The flower illustrated in Fig. 1 (5) provided a clue to probable derivation of the 4-merous flower (Fig. 1 (6, 7)) from a primitive pentamerous form: one of the four sepals was the result of the fusion of two adjacent segments. One of the calyx segments in this flower was petaloid.

Several instances of reversion to primitive pentamery were recorded. Fig. 2 (1–4) gives the floral diagrams of some of them. In these flowers, petaloid staminodes were located opposite and internal to a petal which torsion of the ovary had displaced into the calyx whorl; the petaloid staminodes fill the gap left by the displaced petal. Abortive anthers occur on the petaloid structures.

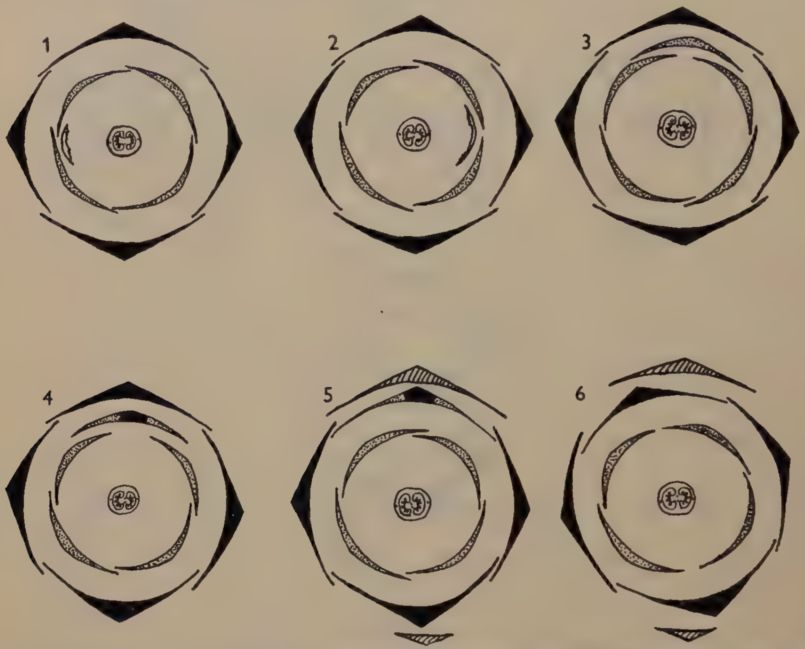

Fig. 3. Floral diagrams of some abnormal flowers showing the displacements of a calyx segment as a bract. (1) Diagram of a 4-merous flower showing a laminar staminode placed inside and between two petals. (2) Same as (1) but the staminode has become more petal-like. (3) Diagram showing the staminode has completely transformed to a petal and occupying a position in the corolla whorl, while one of the outer petals is being displaced from its position. (4) Same as (3) but the displaced petal has become sepaloid by developing chlorophyll in the middle while the fringes are petaloid. (5) Diagram showing the displaced petal now become sepaloid has migrated to the calyx whorl displacing a calyx segment to the outside. (6) Same as (5) but by a twisting of the ovary the displaced calyx comes into a position between two sepals.

In several flowers the petal displaced by a staminode (Fig. 3 (1–3)) occupies a position vacated by a sepal which had been pushed out as a bract; this bract possesses the colour, size and form of a normal sepal (Fig. 3 (4–6)).

Another kind of approach to pentamery is in that a corolla segment lies in the calyx whorl and functions as a sepal, while one of the stamens lies in the gap left in the corolla whorl as a petaloid staminode (Fig. 2 (5, 6)).

Transitional forms. A supernumerary bract placed opposite and exterior to a sepal was observed in six flowers. In one of these flowers, the bract was adnate to the ovary except at the apex (Fig. 4 (1)). The resemblance of this bract to a sepal was very close.

Forty-seven of the seventy-nine flowers with five sepals had also five petals. In all these instances, the fifth sepal was exceptionally large. In only eight of these flowers did the fifth sepal bear a petaloid fringe (Fig. 4 (2)).

Petaloid sepals are illustrated in Fig. 4 (2, 3). They are larger than normal sepals and petals, and possess a green basal area of variable size (shaded black) and a pink petaloid fringe.

Fig. 4 (5) shows a typical petal. A double petal, which was recorded in only two flowers, is illustrated in Fig. 4 (4). The complete transition from a petal to a sepal is presented in Fig. 4 (1–3, 5). All these stages occurred in or interior to the calyx whorl and persisted in the fruits.

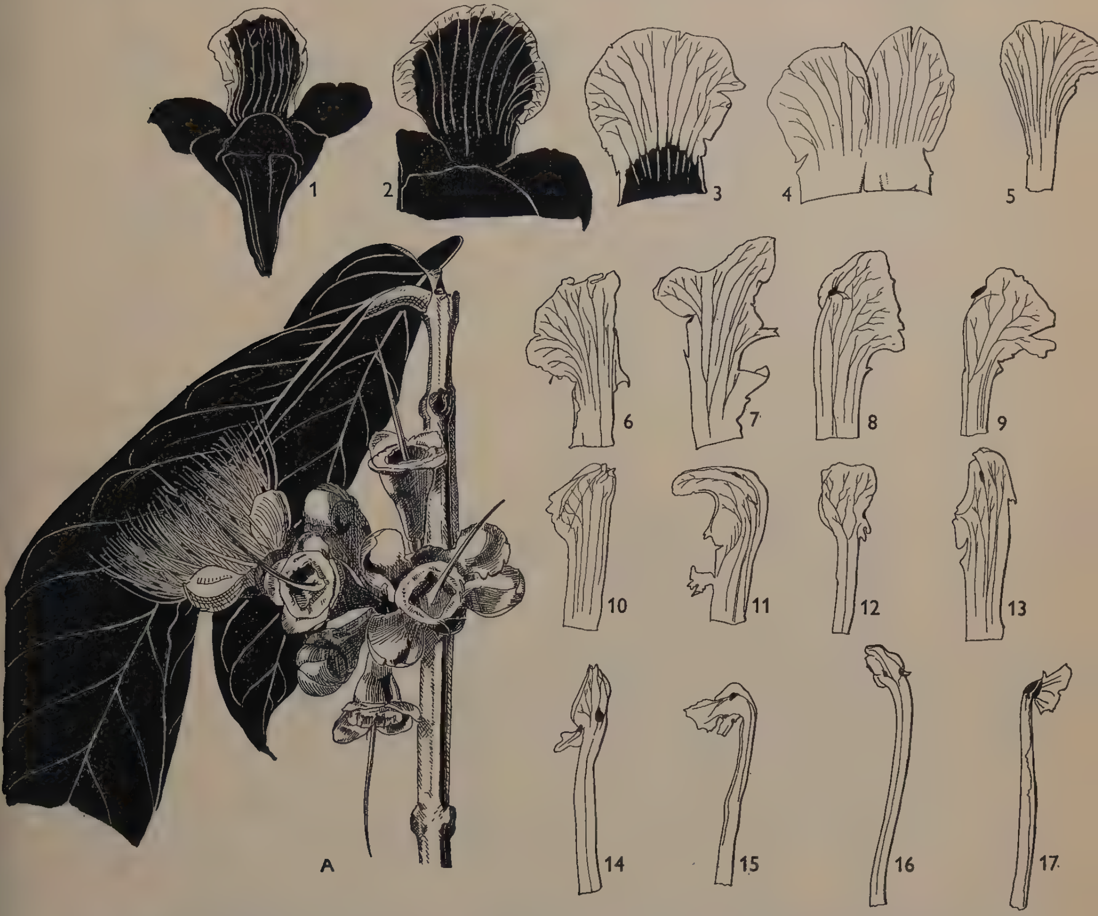

Fig. 4. Some teratological features in the floral parts of the flower. (A) Cluster of flowers showing one flower complete with its floral parts, two in bud and three where the corolla and androecium have fallen off, ×0·66. (1) A petaloid sepal in the calyx whorl where a calyx segment has been displaced as a bract, ×1·33. (2) A typical petaloid sepal, ×1·33. (3) A petaloid sepal where only the basal portion is sepal-like, ×1·33. (4) A double petal, ×1·33. (5) A typical petal, ×1·33. (6)–(13) Petaloid staminodes where only one sterile anther lobe is present, ×1·33. (14)–(17) Staminodes slightly petaloid showing both anther lobes (sterile), ×1·33.

The series of transitional stages between a typical petal and a stamen is indicated in Fig. 4 (6–17) and Fig. 5 (1–5). Sixty of the flowers showed these transitional forms.

Some of the petaloid staminodes (Fig. 4 (6–13)) carried a single anther lobe; others (Fig. 4 (14–17) and Fig. 5 (1–4)) possessed two lobes. Figs. 6 and 7 give detailed camera lucida drawings of transections of these staminodes. The transection in Fig. 6 (1) shows the distribution of vascular bundles (in black) and oil glands. Fig. 6 (2) is a transection of the distal part of the same staminode and shows an anther lobe with fully formed pollen (Fig. 6 (3)). Further transections of staminodes are illustrated in Fig. 7 (A, B). Various types of branching of stamens are shown in Fig. 5 (6–13). An instance of the fusion of two ovaries is seen in Fig. 5 (A).

The appearance of sepaloid bracts on the pedicel of the flower, of petaloid persistent calyx segments in the calyx whorl and of staminodes which resemble petals in the corolla whorl or just inner to it, accompanied by a slight twist in the pedicel of the flower, indicate that transition of members occurs from inside of the flower to the outside in

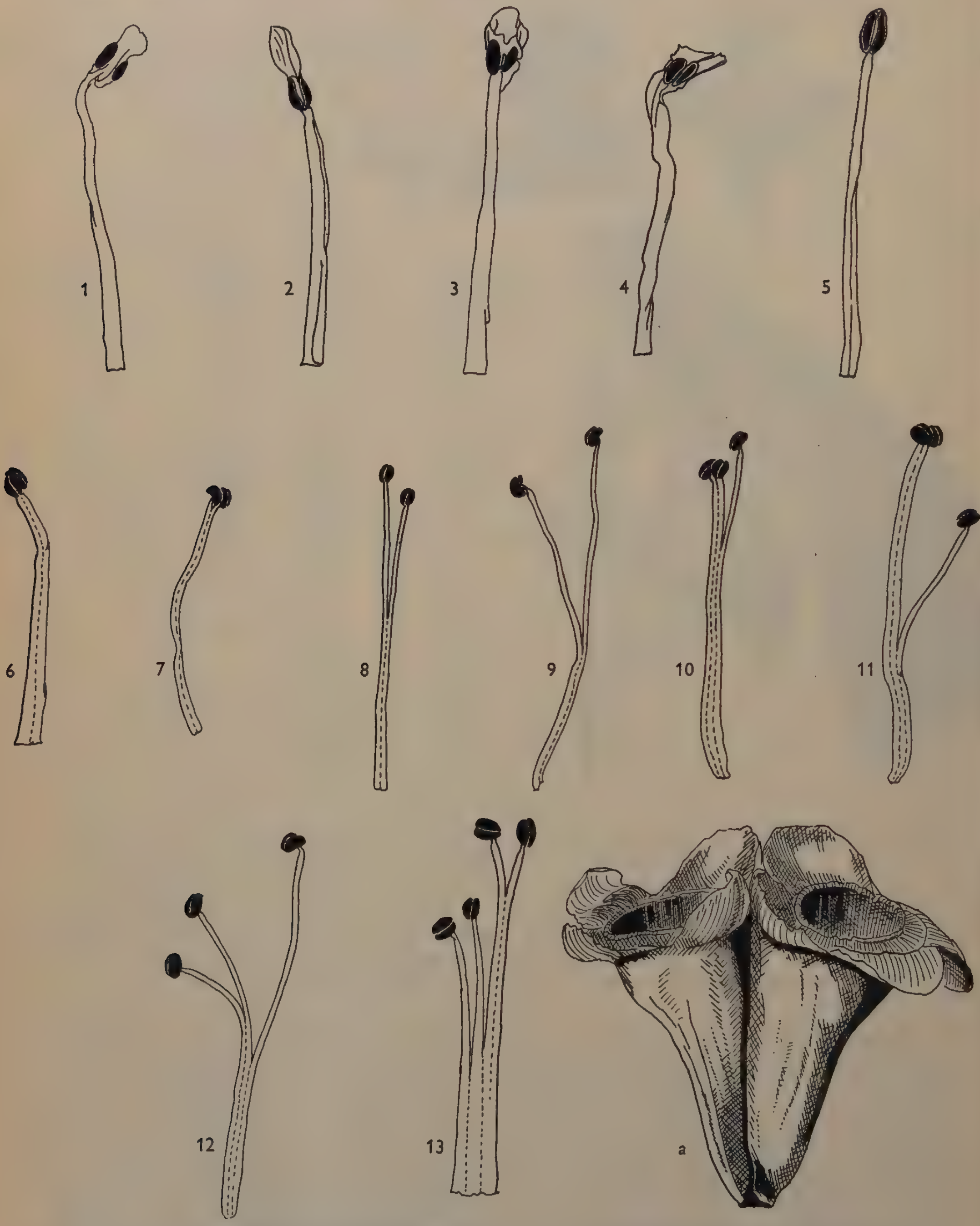

Fig. 5. (a) Two ovaries fused along their length, × 2·25. (1)–(4) Staminodes slightly petaloid carrying the usual anther lobes which probably are fertile, × 2·25. (5) A typical anther, × 2·25. (6)–(13) Stages in the bifurcation, trifurcation and quadrification of the stamens, × 2·12.

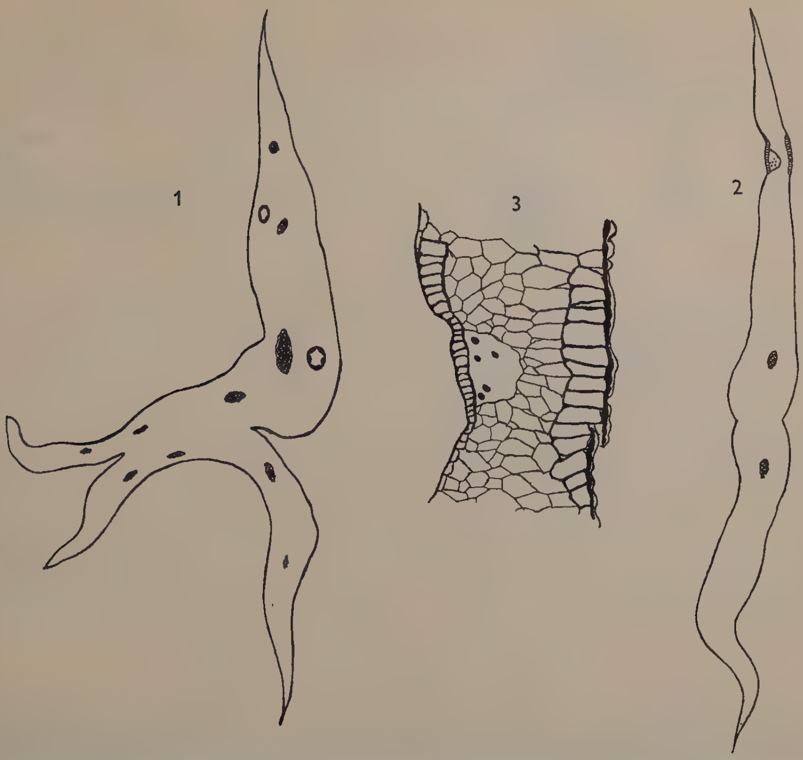

Fig. 6. Diagrams of transverse sections through a typical petaloid staminode. (1) Transverse section through the mid-region of a petaloid staminode drawn in outline showing the distribution of vascular bundles and oil glands, × 13. (2) Transverse section through the apical region of the same staminode drawn in outline showing a fertile pollen chamber, × 13. (3) The pollen chamber of the same staminode showing fertile pollen grains and mechanical tissue, × 38·4.

a spiral course. One type of member does not seem to replace another but add on to it, displacing the other member slightly and increasing the number of segments with a corresponding increase in adjoining whorls (Worsdell, 1916).

SUMMARY

A normal flower possesses a 4-merous perianth, an indefinite number of stamens and pistil consisting of two carpels. Variations from this plan have been described and they may be interpreted as instances of reversion.

There is a correlation between the variation in the different parts of the flower. An increase in one whorl is accompanied by a corresponding increase in other whorls.

Branched stamens were observed in all flowers and bifurcated petals in a few. The occurrence of transitional stages from stamens to petals, petals to sepals, and sepals to bracts suggests the staminodal origin of the floral parts.

The replacement of the four-whorled trimerous perianth by a two-whorled pentamerous perianth and ultimately by a two-whorled 4-merous perianth is suggested. Meristic variation has resulted from the transformation and displacement of flower parts.

ACKNOWLEDGEMENT

The writer wishes to express his gratitude to Dr M. F. Chandraratne for his valuable suggestions and recasting the manuscript.

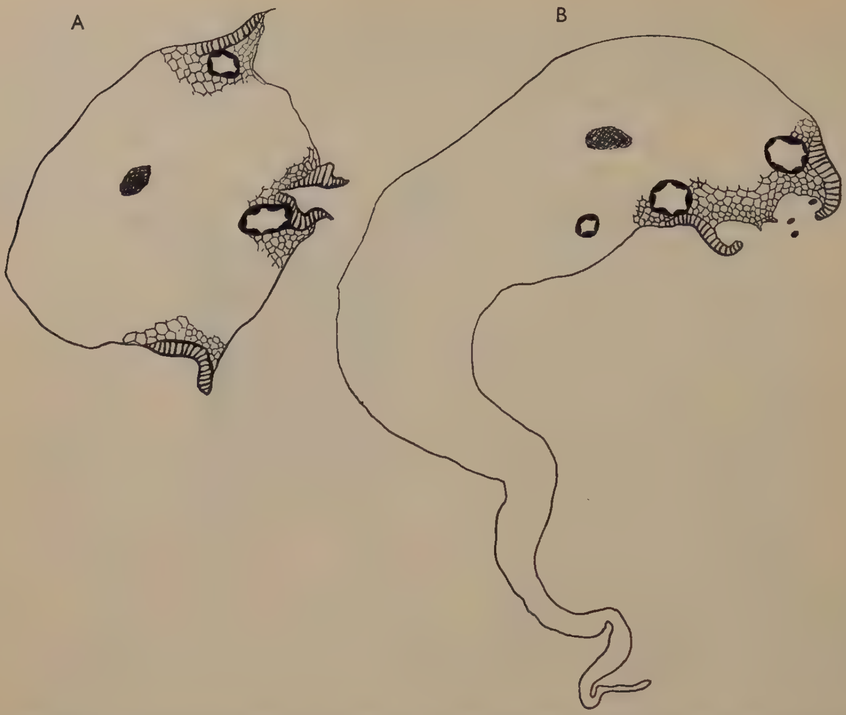

Fig. 7. Diagrams of transverse section through two staminodes. (A) Transverse section through an anther lobe showing only four strands of mechanical tissue and no pollen, × 37·7. (B) Transverse section through a petaloid staminode which carries only one anther lobe bearing fertile pollen, × 37·7.

Cytological and taxonomic observations on some members of the Cyclosorus parasiticus complex.[1] By G. Panigrahi and I. Manton

(With Plate **60** and 7 Text-figures)

[Read 7 November 1957]

INTRODUCTION

Species of the *Cyclosorus parasiticus* complex are among the most abundant path-side weeds in many parts of the old (and new) world tropics, but they are well known to be difficult to deal with taxonomically. There are numerous closely related species, many of which are difficult to distinguish from one another with certainty in the field or as incomplete specimens in herbaria, and there are also cytological complications. Thus Manton & Sledge (1954) showed that while several of the commonest species in Ceylon and Malaya are tetraploid there is at least one diploid, and species-hybrids both triploid and tetraploid are not uncommon. It therefore seemed a good opportunity to use the collection of living plants recently assembled in England from known wild sources to test the suitability of subjecting tropical material to the standard procedures of hybridization followed by chromosome analysis which have already been found to be so useful for studying similar situations among temperate ferns. In this case, however, it was necessary to carry out an extensive survey of the taxonomic literature amplified by search in the national herbaria, concurrently with the breeding programme, since several of the plants used, including the one diploid, were without names when this programme began.

List of species successfully used

(1) *C. repandulus* (v.A.v.R.) Ching (probably = *contiguus* (Rosenst.) Copel.)	P 90	Ceylon	Diploid
(2) *C. parasiticus* (L.) Farw.	P 285	Ceylon	Tetraploid
(3) *C. parasiticus* glandular	P 92	Ceylon	Tetraploid
(4) *C. jaculosus* (Christ) H.Ito	P 199	Ceylon	Tetraploid
(5) *C. subpubescens* sensu Holttum (1954)	—	Singapore	Tetraploid
(6) *C. sumatranus* sensu Holttum (1954)	—	Singapore	Tetraploid
(7) *C. dentatus* (Forsk.) Ching	—	Madeira	Tetraploid

We have fortunately not needed to describe any new species since names corresponding closely to each of our stock plants have been found. We do not claim that the names selected would necessarily be the final ones if a formal taxonomic revision of the genus were being undertaken, but we have been at pains to ensure that they are unambiguous in the sense of enabling a local botanist to identify our material and repeat our results. For this reason we have sometimes accepted the nomenclature of a recent local flora directly related to our plants rather than risk confusion by introducing innovations even on grounds which we believe to be valid. On other occasions we have retained a name based on a type specimen which we have consulted even though we may have reason to think it perhaps a later synonym of a type which we have not consulted. To avoid gross misconceptions on our part we have, however, taken the precaution to submit pressed material of all our main types to Mr A. H. G. Alston of the British Museum under whose advice we have compiled the list on p. 729. This includes all the material which was successfully incorporated into the breeding programme, but excludes a few species which could not be crossed with others even after repeated attempts. Since, however, it may be important to know that each of our named types is in fact in origin only a single plant gathered wild and sent alive to England, we have added the country of origin and the original collector's number (second column) to the list to facilitate reference back to Manton & Sledge (1954) in which the chromosome counts and other details are recorded.

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[1] This work represents part of a thesis submitted for the Ph.D. of the University of Leeds by G. Panigrahi. The experimental and observational work was completed in Leeds during the two calendar years July 1952–July 1954 by him under the direction of the senior author, I. Manton, who has also been responsible for preparing this part of the work for publication after the return of the junior author to India.

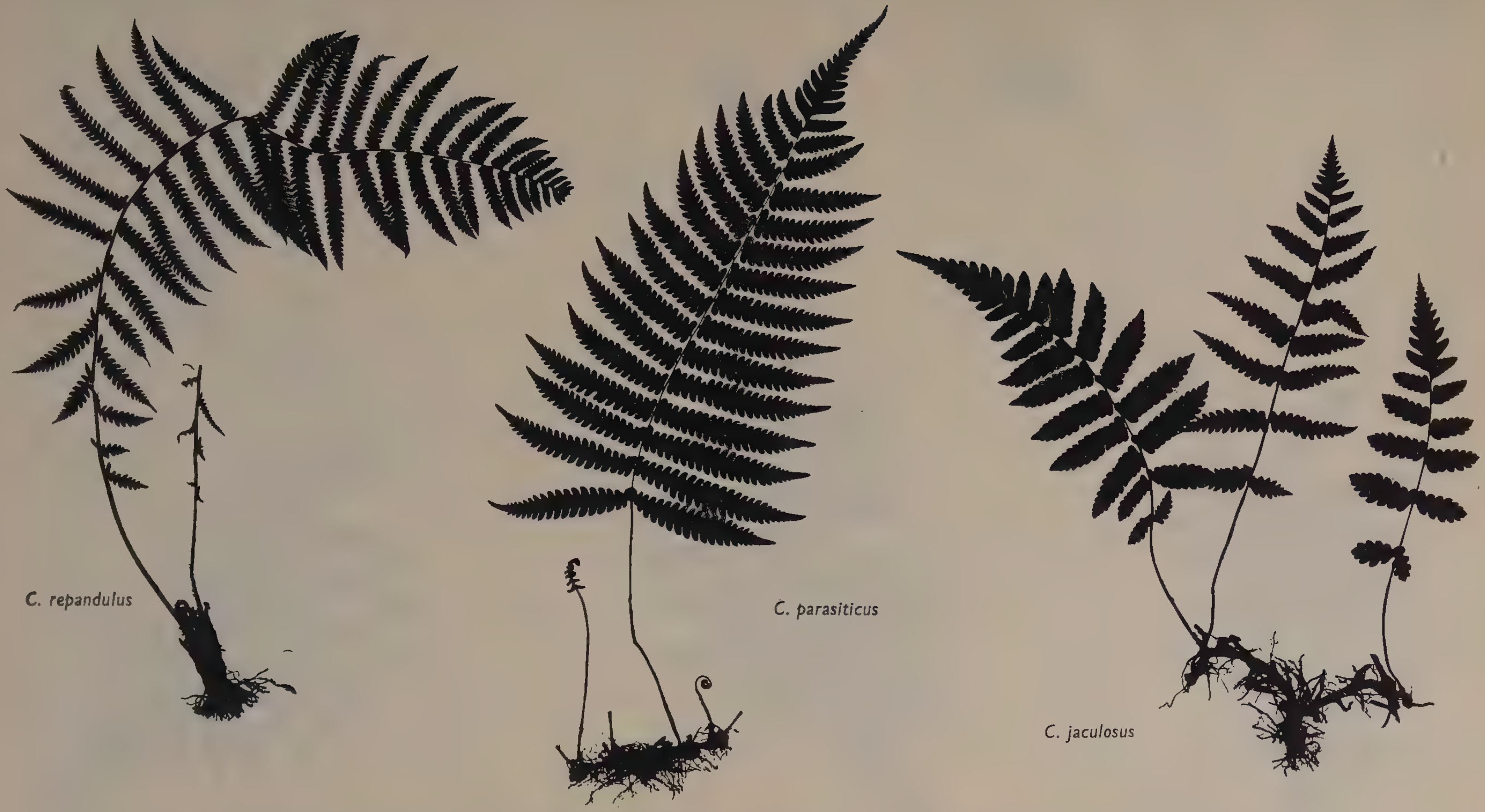
Material and methods

Each of the seven specimens listed above had been successfully established in cultivation either at Kew or in Leeds before this programme began, having been sent to England as an adult wild plant. Those from Ceylon and Madeira (items 1, 2, 3, 4 and 7) had been personally collected by Prof. I. Manton and Dr W. A. Sledge during the Leeds University expeditions to Ceylon (1950) and Madeira (1949); those from Singapore (items 5 and 6) had been personally collected by Prof. R. E. Holttum of the University of Malaya. In each case the stock plant served as a source of spores for the breeding programme, all of which was carried out in Leeds. The stock plants were also used for the morphological observations required for identifications, though these were supplemented by study of spore-produced descendants raised in Leeds, and in most cases by additional information relating to the species in the wild condition. Herbarium specimens of the stock plants and their descendants have been retained for reference; those in the possession of the junior author may be consulted on application to the Shillong Herbarium of the Botanical Survey of India, those in the possession of the senior author will ultimately be deposited at Kew.

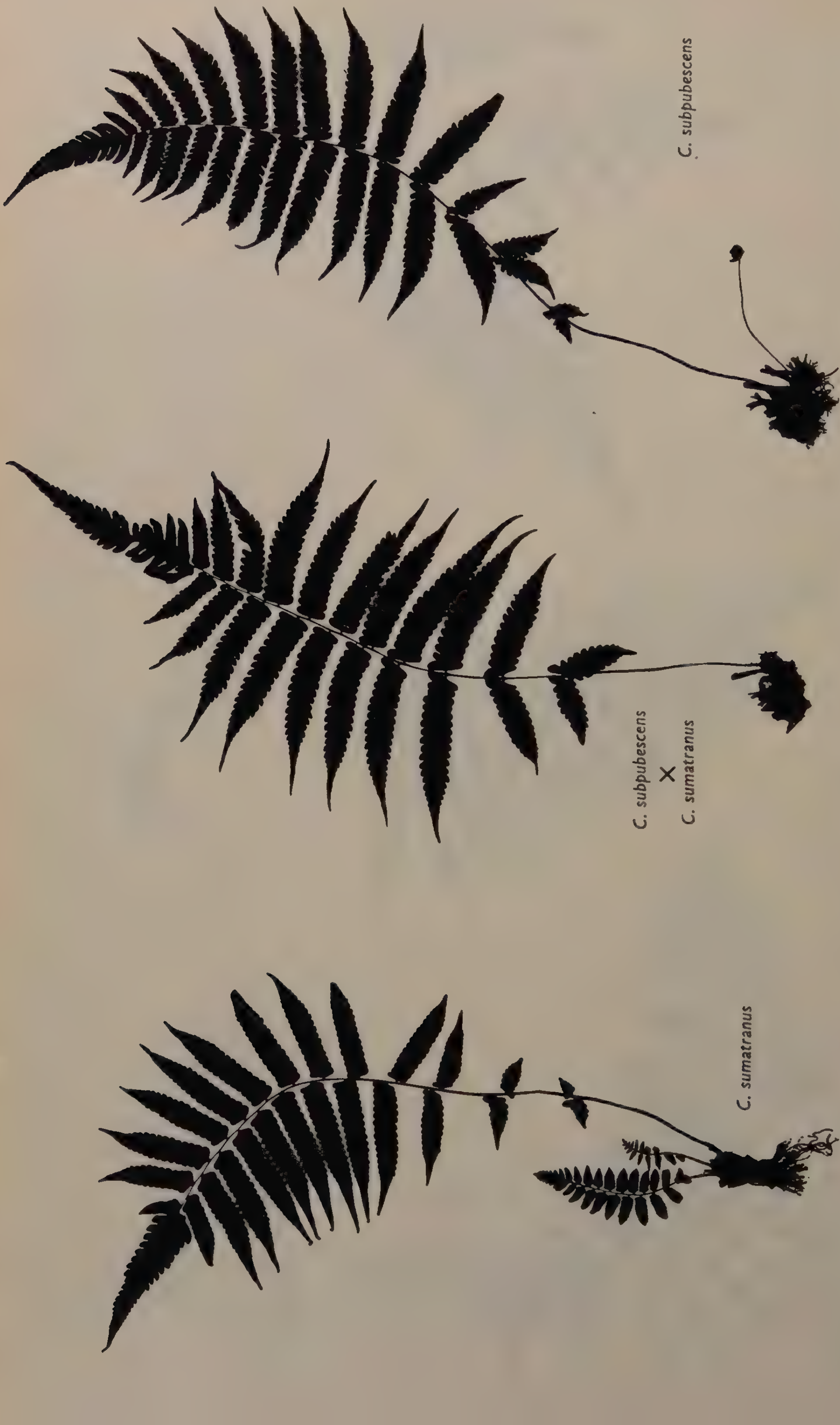
The methods used have been essentially the same as in other work of this kind carried out in Leeds (cf. Manton, 1950; Walker, 1955), except for the need for tropical conditions. In a moist greenhouse kept at 60–80° F. throughout the year most of these species grow rampantly. Prothalli were raised on sterilized compost in 2 in. pots covered with clock glasses and enclosed in a covered frame in the same house. They were ready for use in 2–3 months from sowing. For every species, prothalli required as females were pricked out some weeks before use to minimize the risk of self-fertilization, but in this material it was never possible to avoid entirely the production of antheridia on female gametophytes since they are commonly found at all ages and even on the central cushion among the archegonia; very large numbers of prothalli had therefore to be employed and the progeny rigorously selected to discard accidental homozygotes.

Fortunately the growth of young sporophytes is rapid. In the winter months, November–March, it is not profitable to attempt hybridization owing to lack of light, but at other times in favourable cases young sporophytes can be detected by the emergence of the first leaf in 17 days from insemination and they usually become sporangiferous within 12 months and often, with spring inseminations, by the end of the summer in the same year. This speed of development makes breeding work with these tropical ferns in fact much easier than with ferns of comparable size—e.g. *Dryopteris* (Walker, 1955)—from temperate regions.

The cytological methods used are those of Manton (1950), except for the root-tip squash technique which was modified from Tjio & Levan (1950) and Meyer (1952). This involves the preparation of a saturated aqueous solution of hydroxyquinoline by warming for 10–15 min. at 60° C. On cooling, this solution is diluted with an equal volume of water and the severed root-tips are treated with it for 4 hr. in a tube kept cool under a running tap. After this treatment, which causes chromosome shrinkage, the root-tips may either be stained at once in saturated aceto-orcein or fixed in Carnoy or acetic alcohol with or without subsequent storage in a refrigerator. The most successful treatment was with Carnoy's fixative in the proportions of 4:3:1 absolute: acetic: chloro-

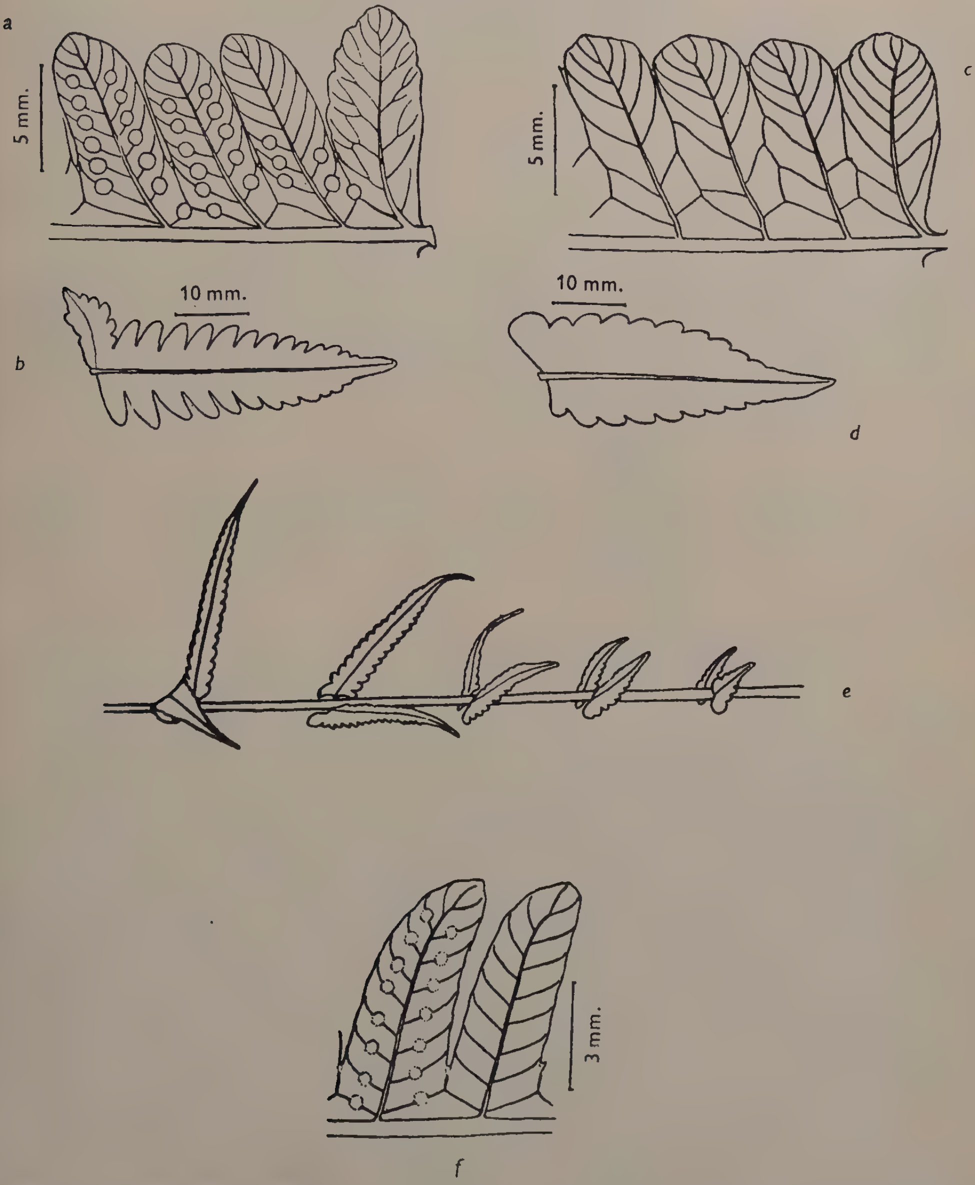


Text-fig. 1. Silhouettes (⅙th natural size) of plants of comparable age (14–15 months) from the three Ceylon taxa, showing the rhizome characters and other morphological differences. *C. repandulus* is diploid, the others are tetraploid; for further description see text.



Text-fig. 2. Silhouettes ($\frac{1}{6}$th natural size) of plants of comparable age of the two Malayan taxa and the hybrid between them. The hybrid combines the rhizome characters of one parent (*C. subpubescens*) with the pinna cutting of the other (*C. sumatranus*).

form used for 12 hr. or longer if stored at 4° C. The squashing process involves prolonged boiling in aceto-orcein until the volume of this reagent is reduced to about a quarter. The roots are then comminuted on a slide with needles and squashed, after gentle warming under a cover-slip, with considerable manual pressure (Panigrahi, 1955). Successful preparations are finished in the usual way as for other types of squash preparation (cf. Manton, 1950, Appendix I).



Text-fig. 3. Drawings showing the range of difference in the characters of venation and depth of cutting of the pinnae to be found in the complex (after Holttum, 1954). *a*, *b*: *C. subpubescens* sensu Holttum, showing 1 pair of anastomosing veins and cutting of pinnae towards the costa about ½. *c–e*: *C. sumatranus* sensu Holttum, with 2½ pairs of anastomosing veins and cutting of pinna towards the costa about ¼. *f*: *C. contiguus*, showing 1 pair of anastomosing veins and depth of cutting of pinna towards the costa about ¾; this species is either a synonym of *C. repandulus* or very similar to it in leaf characters (for further details see p. 735).

Table 1

	C. repandulus (P 90, Ceylon)	*C. parasiticus* (P 285 and P 92, Ceylon)	*C. jaculosus* (P 199, Ceylon)	*C. subpubescens* (Singapore)	*C. sumatranus* (Singapore)	*C. dentatus* (Madeira)
Rhizome	**Erect**	**Wide creeping**	**Wide creeping**	Short creeping	**Erect**	Short creeping
Lower pinnae	Reduced	**Not reduced**	Reduced	Reduced	Reduced	Reduced
Frond apex	Not pinna-like	Not pinna-like	Pinna-like	Pinna-like	Pinna-like	Not pinna-like
Depth of cutting of pinna segments towards costa	**c. ¾**	c. ½	c. ½	c. ½	**c. ¼**	c. ½
No. anastomosing vein pairs	1	1	1	1	**2½**	1–1½
Pubescence on lower surface of rachis	**Dense covering needle-like 1 mm. long hairs**		Hairs very short (mostly **1/5th mm.**)	Hairs long spreading (**1 mm.**)	Hairs minute (mostly about **1/10th mm.**)	Hairs spreading ½ mm.
Anthocyanin on stipe	**Absent**	Present	Present	Present	Present	Present
Glands	—	Absent P 285, present P 92	—	—	—	—
Spores	**34·9 × 23·3 μ**	40·2 × 28·9 μ (P 92) 40·5 × 28·1 μ (P 285)	39·4 × 29·1 μ	40·3 × 27·8 μ	40·3 × 26·7 μ	**37·3 × 30·9 μ**

Morphology of the plants

Morphological descriptions of the species listed on p. 729 will be found in the following works:

(*a*) *C. parasiticus* and *C. dentatus* are described fairly fully in Ching's Monograph (Ching, 1938). The *C. parasiticus* description applies very closely to our material since the type specimen (Osbeck in Stockholm's Riksmuseet) came from China, and Ching's description refers in detail to the Indian and Chinese regions. The type specimen of *C. dentatus*, however, came from Arabia (Forskal), and though Ching quotes a statement from Christensen regarding the prevalence of this species in continental Africa, Ching did not actually cite a specimen from Madeira (the source of our material). On that island there is only one species of *Cyclosorus* (formerly known as *Nephrodium molle*), and in accepting *C. dentatus* as the most probable modern name to apply to it we do not wish to express any views as to whether the Madeira populations are or are not identical in all respects with those of China and the Indian regions.

(*b*) *C. subpubescens* and *C. sumatranus* in the sense used here are described, and some details illustrated by line drawings, in Holttum's recent fern flora of Malaya (Holttum, 1954). It should, however, be pointed out here that the name *C. subpubescens* seems to be used in a rather different sense by Ching (1938) and by Holttum (1954), and in following the latter we merely wish to record the identity of our Malayan material in all respects with that described in the flora and not to express views as to what the correct name should be.

(*c*) For *C. jaculosus* and *C. repandulus* the original descriptions are in Christ (1904) and van Alderwerelt van Rosenburg (1924) respectively, though in both cases these can be supplemented to a limited extent by recent floras. For *C. jaculosus* there are a number of drawings (accompanying a Japanese text) in Ito (1938), while Holttum (1954) gives drawings and a description of leaf characters which fit *C. repandulus* very closely, though under an older name as *C. contiguus*. Unfortunately Holttum's account does not mention the rhizome which we regard as essential to the identification of our species. While therefore we regard it as highly probable that *C. contiguus* and *C. repandulus* are synonyms, in which case *C. contiguus* (Rosenstock, 1917) would be the valid name, we are reluctant to take this step on incomplete evidence. For this reason we are retaining the name *C. repandulus* to refer to our plant (P90), as previously quoted by Manton & Sledge (1954), but if this is understood, and the additional morphological facts listed below are included, Holttum's description of *C. contiguus* could be used to express our species.

In view of all this literature we do not propose to redescribe the species to which our stock plants have been referred except in tabular form and with a few diagrams to illustrate the type of characters involved. These will be found in Text-figs. 1–3, and a list of the more important morphological details which we have found most useful in comparing the living plants with each other and with their hybrids is given below. The distribution of these characters amongst our taxa is summarized in Table 1, with the more important diagnostic characters indicated in black type. From this it will at once appear that the diploid, for example, is readily distinguishable from the tetraploids by its erect rhizome, absence of anthocyanin, small spores, and greater depth of cutting of the pinnae. The complete list of the more important characters is as follows:

(1) Rhizome erect or creeping (cf. Text-fig. 1).

(2) Lower pinnae gradually reduced or not (cf. Text-fig. 1).

(3) Tip of frond forming a distinct terminal pinna (cf. Text-fig. 2) or gradually narrowed to a pinnatifid apex (cf. Text-fig. 1).

(4) Depth of cutting of the pinnae towards the costa (cf. Text-fig. 3).

(5) Number of pairs of anastomosing veins at the base of the pinna-segments (cf. Text-fig. 4).

(6) Degree and nature of pubescence (especially the length of the hairs).

(7) Presence or absence of anthocyanin pigment in the stipe.

(8) Presence or absence of orange-yellow glands.

(9) Size of the spores and sometimes their shape or markings.

Certain of these characters, notably number (7) concerning anthocyanin pigment, may be much more obvious in life than in a herbarium specimen, and their importance here has been in the early age at which they become visible and their consequent value for the early detection of homozygotes in suitable crosses. Other characters, especially the direction of growth of the rhizome, may be impossible to determine until a plant is more than a year old and they cannot be observed in incomplete herbarium specimens. In our experience, however, rhizome characters may be of very great value in distinguishing these species and we wish to stress their importance. Spore characters (size, shape or markings) have not been extensively used in this group (though cf. Ito, 1938), but we believe them to be reliable where differences are shown; our observations here, however, necessarily refer in detail to our own research plants and perhaps do not include all the range of variation detectable in wild populations.

The hybridization programme

The programme as planned involved the setting up of hybrids in all possible combinations between the one diploid (*C. repandulus*) and the five tetraploid species. Only certain combinations, however, proved to be obtainable, and after numerous attempts at the full programme the yield in crosses clearly attested as such was as shown in Table 2.

Table 2

Successful triploid hybrids	Prothalli used	Hybrids obtained	Meiotic analyses (no. plants)	(no. cells)
1. *C. repandulus* ♀ × *C. parasiticus* ♂ (2n, Ceylon) (4n, Ceylon)	48	10	4	7
Reciprocal cross	72	0	—	—
2. *C. repandulus* ♀ × *C. parasiticus* glandular ♂ (2n, Ceylon) (4n, Ceylon)	24	6	5	10
Reciprocal cross	*c.* 50	0	—	—
3. *C. repandulus* ♀ × *C. dentatus* ♂ (2n, Ceylon) (4n, Madeira)	18	5	3	8
Reciprocal cross	25	0	—	—
4. *C. repandulus* ♀ × *C. subpubescens* ♂ (2n, Ceylon) (4n, Singapore)	*c.* 100	0	—	—
Reciprocal cross	*c.* 100	1	1	9
Successful tetraploid hybrids				
5. *C. sumatranus* ♀ × *C. subpubescens* ♂ (4n, Singapore) (4n, Singapore)	25	4	3	9
6. *C. jaculosus* ♀ × *C. sumatranus* ♂ (4n, Ceylon) (4n, Singapore)	6	1	1	7
7. *C. subpubescens* ♀ × *C. jaculosus* ♂ (4n, Singapore) (4n, Ceylon)	20	1	1	incomplete

A chromosome count is the easiest and most certain way of diagnosing a successful hybrid in the case of crosses expected to be triploid, and root-tip counts were in fact made of all the attested triploids. In the case of tetraploid crosses a chromosome count is uninformative since there is no difference in chromosome number between hybrid and parents, and the only guide here is morphology in young plants and meiotic behaviour or spore sterility in old ones. A report on meiosis will be given in the next section, but it can be stated at once that all of the attested hybrids, both triploid and tetraploid, showed a very high proportion of mis-shapen and aborted spores.

A detail which was not expected and which is perhaps worth comment at this point is the marked difference which was encountered on several occasions in the ease of production of species hybrids in reciprocal directions. The figures for tetraploid crosses are less precise than for triploid and we have not quoted the unsuccessful attempts which were in each case made to establish hybrids in the reverse direction to those quoted. For the triploid crosses where attempts were more systematically carried out it was apparently impossible to combine *C. repandulus* with either *C. parasiticus* or *C. dentatus*, except with the diploid as source of female gametes. Combinations which failed altogether in both directions, even after repeated attempts, were *C. repandulus* (diploid) with each of the tetraploid species *C. jaculosus* and *C. sumatranus*. At the tetraploid level time did not permit all desirable hybrids to be attempted, and there is therefore no data on the possibility or otherwise of combining *C. parasiticus* or *C. dentatus* with the other tetraploid species. A diagram summarizing these facts will be found in the section on cytology (p. 739).

Morphology of hybrids

Many of the hybrids listed in Table 2 showed such a close resemblance to one only of the two parent species that without the cytology or the spore characters they could have been mistaken for members of the pure species. This behaviour, which could be very misleading to a herbarium botanist without direct knowledge of the parentage of a dried plant, depends upon the fact that several of the more striking criteria used for distinguishing the species are completely recessive when combined into F_1 hybrids. This does not necessarily mean that these characters would segregate as simple allelomorphs if later generations could be obtained, but it does mean that certain characters of one species may fail to find any immediate visible expression in a first-generation hybrid with another species. The more important characters which behaved in this way in our cultures were:

(1) *Rhizome.* Erect was recessive to creeping in all combinations, i.e. in all the hybrids listed as 1–6 in Table 2 and involving either *C. repandulus* or *C. sumatranus* with other species.

(2) *Anthocyanin.* Absence of pigment was recessive to presence of pigment in all hybrids involving *C. repandulus* with other species, i.e. items 1–4 in Table 2.

(3) *Lower pinnae.* Gradual reduction in length of lower pinnae was recessive to absence of reduction in crosses involving *C. parasiticus* (items 1 and 2 in Table 2).

(4) *Glands.* Absence of glands was recessive to presence of glands in the one hybrid involving glandular *C. parasiticus* (item 2 in Table 2).

Since most of the more conspicuous characters of the diploid species *C. repandulus* thus behave as recessives, all hybrids involving this species, i.e. all the triploids, show very little external sign of the presence of this species in their parentage (compare, for example, Text-figs. 1 and 4), a fact which, however, greatly assisted the early detection of accidental selfs in the hybridization experiments since, with *C. repandulus* prothalli, selfed sporophytes stand out at once by their absence of anthocyanin.

Other characters, especially those of a quantitative kind such as degree of cutting of the pinnae, length of hairs in the pubescence, number of anastomosing veins,[1] did not show complete dominance but were in an intermediate condition in the hybrids compared with the parental types.

Cytology of the hybrids

The monoploid chromosome number in the genus *Cyclosorus* is well known to be 36 (cf. Manton, 1953; Manton & Sledge, 1954), and since the basic counts on all the plants used here had already been completed in time to be quoted in the latter publication it is not necessary at this stage to demonstrate them further in detail, though one squash from a diploid root showing the seventy-two somatic chromosomes is included in Pl. **60**, fig. *a*, for comparison with the triploid (Pl. **60**, fig. *b*; Text-fig. 5*b*).

In addition to the root-tip counts which were made at an early stage as a test of heterozygosity in triploids, meiosis has been studied in representatives of each type of hybrid, on the scale indicated in the last two columns of Table 2. Owing to the late date at which sufficiently mature hybrid plants began to become available, the number of fully analysed cells was necessarily restricted below the requirements for fully significant quantitative comparisons. The qualitative observations, on the other hand, are fairly clear since they can be based on fewer cells. The general pattern of behaviour found can be summed up as follows:

(1) All the hybrids listed could be shown to owe their defective spores to the presence, among other things, of a large number of unpaired chromosomes in the spore mother cells at the first meiotic division.

(2) In the triploid hybrid between *C. repandulus* and *C. dentatus* from Madeira univalents predominated, and often all 108 chromosomes were in this condition (cf. Pl. **60**, fig. *c*; Text-fig. 5*a*). A few pairs are, however, occasionally formed with a maximum number of 20 bivalents seen in one case[2] (Pl. **60**, fig. *d*; Text-fig. 5*d*).

(3) In contrast with this all the other triploids examined showed approximately equal numbers of pairs and univalents with only minor deviations. Thus in one plant of *C. repandulus* × *C. parasiticus* involving P92 (*C. parasiticus* glandular) nine out of the

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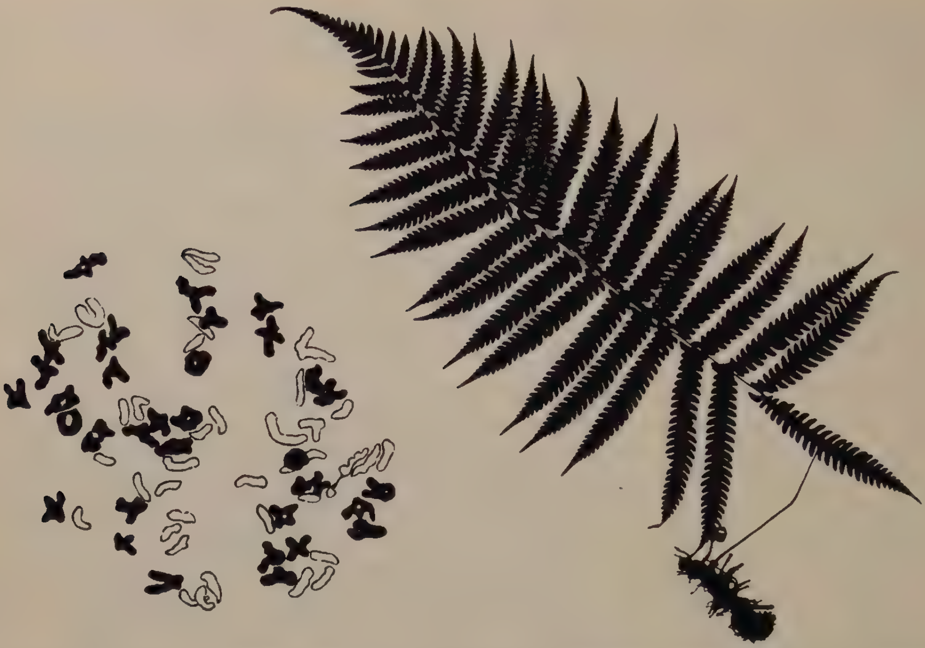
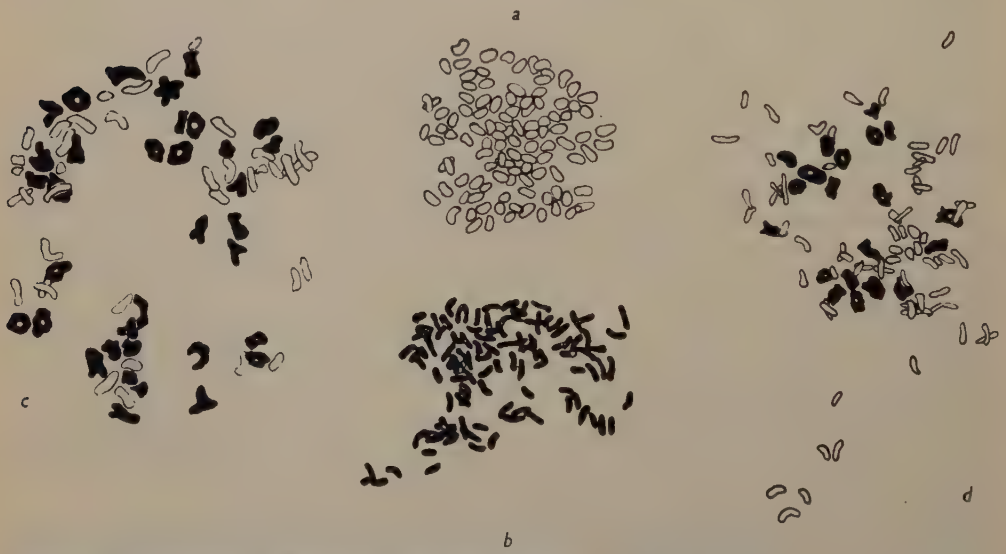
[1] In young hybrid plants involving *C. sumatranus* the 2½ pairs of anastomosing veins of this species appear to be completely dominant, but with older hybrid plants venation is more nearly intermediate between that of the two parents.

[2] Among the eight best cells from one plant of this combination, five showed 108 univalents, two showed 5 pairs + 98 univalents and one showed 20 pairs + 68 univalents.



Text-fig. 4. Silhouette ($\frac{1}{6}$th natural size) of a triploid hybrid, between *C. repandulus* and *C. parasiticus* (cf. Text-fig. 1), showing dominance of the rhizome and frond characters of *C. parasiticus*, but its hybrid nature is attested both by its chromosome number ($3n = 108$) and by the irregular pairing at meiosis. The chromosome diagram gives the analysis of the cell of Pl. **60**, fig. *e*, as 36 pairs (black) and 3 univalents (outline). (Note $n = 36$.)



Text-fig. 5. Explanatory diagrams to cells from triploid hybrids included in Pl. **60**, all × 1500. *a–c*: the triploid between *C. repandulus* and *C. dentatus* (Madeira); *a*, a somatic cell from a root-tip squash with 108 somatic chromosomes (cf. Pl. **60**, fig. *c*); *b*, meiosis in a spore mother cell with complete failure of pairing (cf. Pl. **60**, fig. *b*); *c*, meiosis in another cell of the same plant as *b* showing the maximum extent of the pairing encountered, i.e. 20 pairs in black and 68 univalents (cf. Pl. **60**, fig. *f*); *d*: the triploid between *C. repandulus* and *C. subpubescens* sensu Holttum showing pairing very like that of Text-fig. 4, namely 1 trivalent and 35 pairs in black, 35 univalents in outline (cf. Pl. **60**, fig. *d*). (Note $n = 36$.)

ten cells analysed gave exactly 36 pairs and 36 univalents (cf. Pl. **60**, fig. *e*; Text-fig. 4), but the tenth cell was discordant giving 1 trivalent, 30 pairs and 45 univalents. A second plant, involving P285 (*C. parasiticus* non-glandular), gave 34 bivalents and 38 univalents in each of the 7 analysed cells. For the other triploid combination, namely *C. repandulus* × *C. subpubescens* (Singapore), the analysis of the two best cells gave 35 bivalents and 34 bivalents + 1 trivalent (cf. Pl. **60**, fig. *f*; Text-fig. 5*c*), the remaining chromosomes being unpaired. No significance can be attributed to these relatively slight differences without knowledge of a far larger number of plants, and many more accurately analysed cells.

(4) For the tetraploid hybrids, all the analysed cells (7) of the *C. jaculosus* (Ceylon) × *C. sumatranus* (Malaya) cross gave 36 pairs and 72 univalents (cf. Pl. **60**, fig. *h*; Text-fig. 6*b*). For the *C. sumatranus* (Malaya) × *C. subpubescens* (Malaya) cross the best cell (Pl. **60**, fig. *g*; Text-fig. 6*a*) gave 37 bivalents and 70 univalents. The third tetraploid, that between *C. subpubescens* (Malaya) and *C. jaculosus* (Ceylon), could not be analysed in detail, and the only statement possible is that both pairs and univalents were present.

These facts are perhaps conveniently summarized in the following diagram:

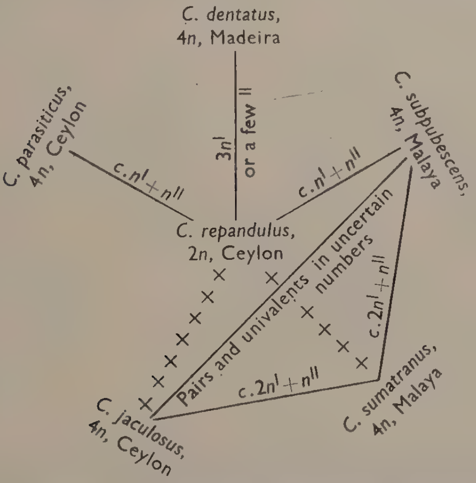
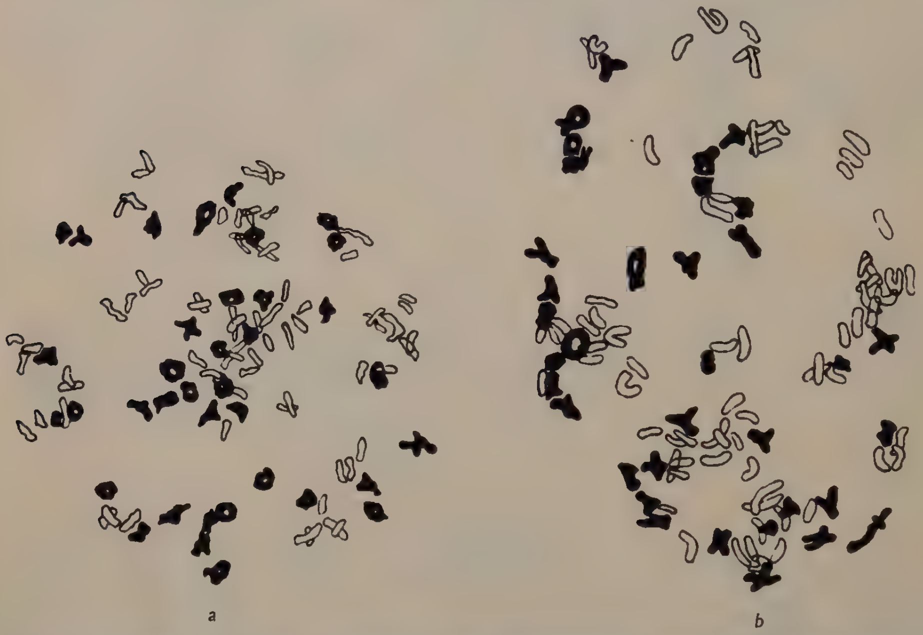

C. dentatus, 4n, Madeira
C. parasiticus, 4n, Ceylon
C. subpubescens, 4n, Malaya
$3n^{\mathrm{I}}$ or a few II
c.$n^{\mathrm{I}}+n^{\mathrm{II}}$
c.$n^{\mathrm{I}}+n^{\mathrm{II}}$
C. repandulus, 2n, Ceylon
Pairs and univalents in uncertain numbers
c.$2n^{\mathrm{I}}+n^{\mathrm{II}}$
c.$2n^{\mathrm{I}}+n^{\mathrm{II}}$
C. jaculosus, 4n, Ceylon
C. sumatranus, 4n, Malaya

Diagram summarizing frequency of pairs and univalents at meiosis in the interspecific hybrids obtained. × × × = attempted crosses which could not be made.

Discussion

The most probable interpretation of the cytological facts summarized in the diagram is that *C. repandulus*, or a form with similar chromosome homologies, is related ancestrally to several of the species involved in this investigation, though possibly not to all. The very low pairing with the chromosomes of *C. dentatus* does not suggest close affinity with that species, and the apparent impossibility of obtaining a hybrid between *C. jaculosus* and *C. repandulus* perhaps denotes the same thing. On the other hand, the nature of the chromosome pairing in the triploids involving *C. parasiticus* and *C. subpubescens* respectively would be entirely in accord with the view that the *repandulus* genome is in fact present in both these species, in each of which it represents half the nuclear complement. Similarly, the pairing in the tetraploid hybrids suggests strongly that *C. subpubescens* has one diploid ancestor in common with *C. sumatranus*, and that *C. sumatranus* has one diploid ancestor in common with *C. jaculosus*. Owing to incompleteness of the breeding programme we lack proof that this common ancestor was in every case *C. repandulus*, but the possibility is there that it could be.

Whether this is true or not, however, it is quite obvious that our one diploid (*C. repandulus* or a form with similar chromosomes) is by itself quite insufficient to provide materials for the formation of such a large number of tetraploid species, and one must believe that additional forms at the diploid level must certainly have existed in the past or may possibly still exist if search could be effectively conducted. Attention has already been drawn to the marked resemblance of several of our hybrids to one only of the two parent species, and if this had been repeated at an earlier evolutionary stage we may in fact find that in certain cases diploid ancestral types may actually have been collected, but that they have not yet been distinguished from their amphidiploid descendants. Careful search in herbaria, with special attention to spore sizes, might therefore in certain cases give information as to the present whereabouts of other diploids.



Text-fig. 6. Chromosome pairing at meiosis in two different sorts of tetraploid hybrids, magnified × 1500. *a*: the cross between *C. sumatranus* sensu Holttum and *C. subpubescens* sensu Holttum, both from Singapore (cf. Text-fig. 2), with 37 bivalents in black and 70 univalents in outline. *b*: the cross between *C. jaculosus* (Ceylon) and *C. sumatranus* with 36 pairs (black) and 72 univalents (outline). (Note $n = 36$.)

In addition, it is very desirable to obtain further information about the known diploid. At present cytological information is confined to Ceylon, in which island the taxon to which we have referred P90 was not previously known to exist. There is no direct cytological information for the type locality (New Guinea), and this is equally lacking for *C. contiguus* which, as stated earlier, may prove to be a synonym for our plant. Ecological information is slightly less scarce, since we can now state (Sledge, personal communication) that *C. repandulus* in Ceylon is a plant of forest clearings.* The same appears to be true of *C. contiguus* in Malaya and Borneo (Holttum, personal communication); human interference is thus likely to be less damaging to it than is often the case. Nevertheless, even with this advantage, and allowing for the fact that *C. repandulus* may actually be present unrecognized in other countries besides Ceylon and New Guinea, there can be no doubt that relatively to the tetraploids this diploid is scarce, although it seems to be spread over a fairly wide area. If the records for *C. contiguus* and *C. repandulus* are added together they represent occasional finds by a few people in New Guinea, Ceylon, Malaya, Borneo and perhaps Madagascar.[1]

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* We are indebted to Dr Sledge for the following new observations made by him on his second visit to Ceylon in the spring of 1954: '*C. repandulus* is much less frequent in Ceylon than *C. parasiticus* from which it is readily distinguished in the field by its erect rhizome (sometimes projecting well above ground level), by its markedly decrescent fronds, by its paler, yellow-green colour and by its much shorter stipes. To judge by the few localities in which I collected it, it favours partially shaded situations such as roadside banks through wooded areas, and forest clearings.'

All these facts indicate a situation which has a lot in common with that recently unravelled in the *Dryopteris spinulosa* complex of Britain (Manton, 1950; Walker, 1955). In both cases we have a complex of inter-related tetraploid species, some of which are very abundant. In both cases we have in the same territory a single diploid which is much less common, but which seems to be related in an ancestral manner to several of the tetraploids. In both cases the diploid, though less frequent, is nevertheless spread over a relatively large area, and it is therefore reasonable to conclude that in both cases the diploid represents the remains of an older population which has suffered reduction.

This close resemblance in the facts revealed by cyto-genetic study of two unrelated fern genera in very different parts of the world may suggest that there must be factors at work in the evolution of a tropical flora which are parallel in their effects to the glaciations and interglacials of temperate latitudes but which must necessarily be different in kind. It is useless to speculate about the factors involved until more detailed knowledge is available about the recent geological and climatic history of tropical countries. It is, nevertheless, clear that the cytotaxonomic study of tropical plants is both possible and rewarding in itself, and that if further pursued it may also illuminate the past history of floras about which very little is known.

Summary

1. Interspecific hybrids have been set up between a diploid species of *Cyclosorus* from Ceylon provisionally identified as *C. repandulus* and three tetraploid species, namely *C. dentatus* from Madeira, *C. parasiticus* from Ceylon (two forms), and *C. subpubescens* from Singapore.

2. Interspecific hybrids have been set up between certain pairs of tetraploid species, namely *C. subpubescens* (Singapore) × *C. sumatranus* (Singapore); *C. sumatranus* (Singapore) × *C. jaculosus* (Ceylon); *C. jaculosus* (Ceylon) × *C. subpubescens* (Singapore).

3. In morphology these F_1 hybrids both triploid and tetraploid showed complete dominance in the expression of some of the morphological characters in which the parents differ and an intermediate condition in others. The more important characters showing dominance were: creeping rhizome versus erect rhizome, presence of anthocyanin pigment on the rachis versus absence of it, uniform length of the lower pinnae versus gradual reduction in length, presence of glands versus absence of these. The more important characters in which simple dominance was *not* displayed (i.e. F_1 hybrids were intermediate between the two parental types) were: depth of cutting of the pinnae, number of anastomosing veins at the base of the pinna segments (in old plants, cf. footnote to p. 737), length of hairs on the lower surface of the stipe.

4. All the hybrids obtained, both triploid and tetraploid, showed a high proportion of aborted spores consequent on irregular meiosis. This was clearly evident even in cases where a preponderance of recessive characters in one parent resulted in a hybrid showing a very close morphological resemblance to the other parent. Spore sterility would therefore be an effective means of detecting hybridity in a herbarium specimen.

5. Chromosome pairing at meiosis has been investigated in all these hybrids in a

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[1] This citation is based on two sheets in the British Museum Herbarium which appear to resemble *C. repandulus* very closely. They are labelled: C. W. Bewsher 71 Madagascar, and J. M. Hildebrant Madagascar.

preliminary way. All show numerous unpaired chromosomes as one factor contributing to spore abortion. In addition, the triploid between *C. repandulus* (Ceylon) and *C. dentatus* (Madeira) showed few or no pairs, indicating rather remote relationship between these two species. The other triploids involving *C. repandulus* with *C. parasiticus* and *C. subpubescens* respectively all showed approximately equal numbers of pairs and univalents, suggesting that the *repandulus* genome is represented in each of the two tetraploid species as half the nuclear content. Among the tetraploid hybrids pairing approximating to n pairs and $2n$ univalents was found in each of the two combinations *C. subpubescens* × *C. sumatranus* and *C. sumatranus* × *C. jaculosus*, suggesting that in each of these pairs of species a diploid ancestor is shared. This ancestor could be *C. repandulus* in one or both cases, though the evidence is insufficient to determine this.

6. Present knowledge of the ecology and geographical distribution of *C. repandulus* is outlined and a method is suggested for searching for the possible existence of other diploids not yet identified.

7. A comparison is made between the *C. parasiticus* complex in the oriental tropics and the situation already partially elucidated by other workers on the *Dryopteris spinulosa* complex in Europe. The resemblance is so close that it seems likely that there are factors operating in tropical floras which are at least as powerful though necessarily somewhat different in kind from those associated with the succession of glacial and interglacial conditions which have so strongly influenced the evolution of floras in temperate regions.

ACKNOWLEDGEMENTS

Very grateful thanks are due to Prof. R. E. Holttum, Dr W. A. Sledge and Mr A. H. G. Alston for help and advice on many occasions, and to Mr F. Ballard of the Kew Herbarium and Prof. H. Lam, Director of the Rijksherbarium, Leiden, for facilitating access to specimens in their charge.

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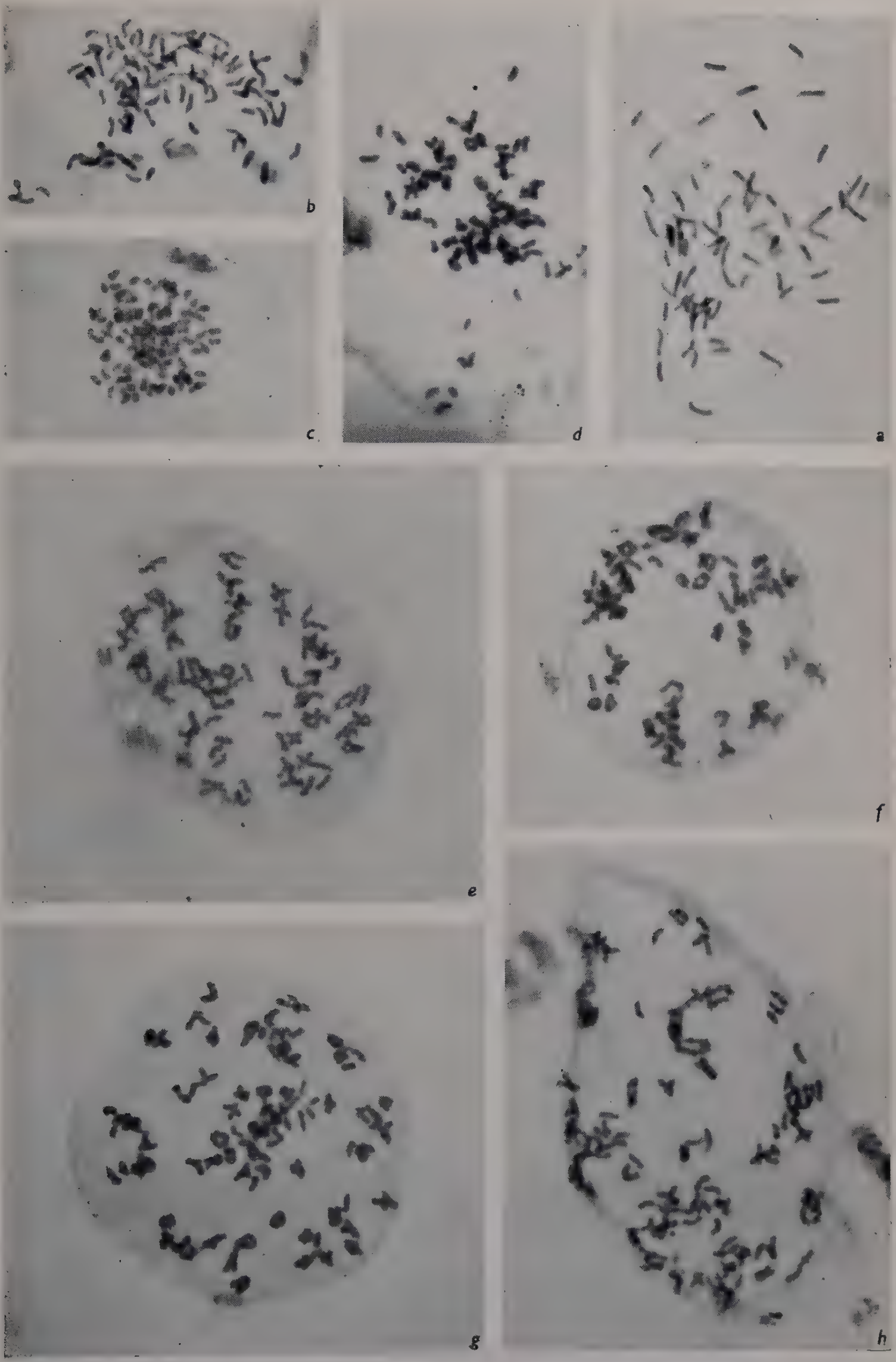
EXPLANATION OF PLATE 60

Photographs of cells from acetocarmine-squash preparations after permanent mounting in Canada balsam. Magnification of Figs. *a* and *b*, × 1500; the remainder, × 1000.

Fig. *a*. Root-tip squash of *C. repandulus* showing the diploid number of somatic chromosomes ($2n = 72$).



Cytology of *Cyclosorus* hybrids.

(*Facing p.* 742)

Fig. *b*. Root-tip squash of a triploid hybrid between *C. repandulus* and *C. dentatus* (Madeira) with 108 somatic chromosomes.

Fig. *c*. Meiosis in the same plant as fig. *b* showing a spore mother cell with 108 unpaired chromosomes at meiosis.

Fig. *d*. Meiosis in another cell of the same plant as figs. *b* and *c* showing slight pairing; for explanatory diagram see Text-fig. 5*d*.

Fig. *e*. Meiosis in a triploid hybrid between *C. repandulus* and *C. parasiticus* showing *n* pairs and *n* univalents; for explanatory diagram see Text-fig. 4.

Fig. *f*. Meiosis in the triploid hybrid between *C. repandulus* and *C. subpubescens* sensu Holttum, with approximately *n* pairs and *n* univalents; for explanatory diagram see Text-fig. 5*c*.

Fig. *g*. Meiosis in the tetraploid hybrid between *C. sumatranus* sensu Holttum and *C. subpubescens* sensu Holttum, both from Singapore, with approximately *n* pairs and 2*n* univalents; for explanatory diagram see Text-fig. 6*a*.

Fig. *h*. Meiosis in the tetraploid hybrid between *C. jaculosus* (Ceylon) and *C. sumatranus* (Singapore) with *n* pairs and 2*n* univalents; for explanatory diagram see Text-fig. 6*b*.

The typification of Polyides and Furcellaria. By KATHLEEN M. DREW,[1]

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(Communicated by R. Ross, F.L.S.)

(With Plates **61–63** and 3 Text-figures)

[Read 7 November 1957]

The genus *Polyides* was erected by Agardh in 1822, and he included a single species *P. lumbricalis* in it. *Furcellaria* was erected in 1813 by Lamouroux, and in this genus he placed *Fucus lumbricalis* var. *alpha* of Turner as *Furcellaria lumbricalis*, and *Fucus lumbricalis* var. *beta* of Turner as *Furcellaria fastigiata*. Both of these generic names have been conserved against *Fastigiaria* Stackhouse erected in 1809 (Papenfuss, 1950, p. 193). At the present time each genus is considered to include but a single species, but the identity of the type material has never been established in either case. The genera *Polyides* and *Furcellaria* are widely separated taxonomically, the former belonging to the Polyidiaceae and the latter to the Furcellariaceae, families which belong to the Cryptonemiales and Gigartinales respectively. These systematic positions rest on considerable differences in details of reproduction and the development of the carposporophyte, but sterile fragments of thalli without the attachment organ cannot be identified with certainty on the basis of external appearance. Sections of the thallus have to be made, and even anatomically the resemblance between the two genera is close.

The similarity between fragments of sterile thalli of *Polyides* and *Furcellaria*, as well as variations in form shown by the latter, resulted in considerable confusion in the early literature. An additional reason for confusion rests in the fact that the Linnean specimens of *Fucus fastigiatus*, described by Linnaeus in 1753, have been considered to be a mixture. Moreover, at an early stage, Dawson Turner concluded that one of the specimens was *Fucus rotundus* (incorrectly as it turns out) and made it *β fastigiatus* of that species. In addition, *Fucus rotundus* of Gmelin was thought to have been incorrectly identified by him with *F. rotundus* of Hudson (but now shown to be correctly so). Yet another reason for confusion is to be found in the changes made by Hudson in the second edition of *Flora Anglica*, changes which were generally accepted by subsequent writers. Finally, doubt about the identity of these algae can be attributed to the brevity of many of the earliest descriptions of these algae. Mis-identifications were inevitable in consequence.

The search for the first validly and effectively published descriptions of entities which might be *Polyides* Agardh or *Furcellaria* Lamouroux leads back to some of these very brief and unillustrated descriptions. The only course therefore was to examine the specimens on which the descriptions and hence the binomials rest. The three specimens described in this paper are all sterile and moreover without the base. It has been necessary therefore to section the material to establish its identity. Unfortunately, sections of such herbarium material are not easy to prepare without soaking in water which induces considerable swelling of the cell walls, distorting the arrangement of the cells. However, the essential details for distinguishing *Polyides* from *Furcellaria* remain sufficiently clear.

Denys (1910) and Rosenvinge (1917) have studied the anatomy of these two genera, which both show the multiaxial type of construction. In transverse sections of both, a clear differentiation into an outermost small-celled cortex and an inner large-celled cortex and a central medulla can be seen. There are, however, differences in detail which are present in sections even within 2 mm. of the growing point. First, the outer small-celled cortex of *Polyides* consists of two to four layers of regularly arranged quadrate or subcylindrical cells, whereas in *Furcellaria* this outer cortex consists of one or occasionally two layers of much longer cylindrical cells. The change to the large-celled inner cortex is much less gradual in *Polyides* than in *Furcellaria*, where cells of an intermediate size are found. While the individual cells of the large-celled inner cortex are essentially similar in both genera, they appear to be more regularly arranged in *Polyides*. Many secondary hyphal filaments develop from the innermost cells of the inner cortex of *Furcellaria* and grow in between the longitudinally running primary filaments of the medulla. These primary filaments of the medulla have thick walls and the cell lumen is small. In *Polyides*, the change from the cortex to the medulla is gradual, the cells becoming longer and narrower and spirally arranged. Rosenvinge (1917, p. 173) writes 'the cells which form the connexion between these filaments (i.e. of the medulla) and the cortical ones are arranged in regular feebly curving rows, running obliquely upwards'. This spiral arrangement is a characteristic feature in sections of living material and can also be seen in sections of herbarium material provided they have not become distorted by swelling of the cell walls in water.

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[1] Now deceased.

A. *The genus* Polyides

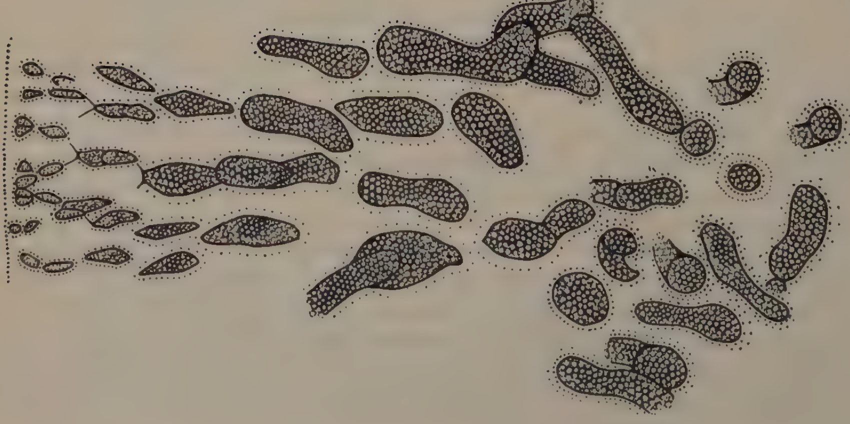
Polyides Agardh, 1822 (syn. *Spongiocarpus* Greville, 1824)

When Agardh erected this genus, he gave a full description which, by references to the 'verrucae nudae spongiosae e filis constitutae fastigiatis, inter quae globuli seminum nidulantur' and also to 'radix scutata', leaves no doubt as to the taxon he was describing. Two years later, Greville (1824, p. 286) erected a genus *Spongiocarpus*, clearly synonymous with Agardh's genus, and later (1830) withdrawn by him in favour of *Polyides*. Greville typified his genus with the *Fucus rotundus* of Turner (=*F. rotundus* Gmelin). Gmelin's plant was clearly *Polyides*, and he cites references to *Fucus rotundus* Hudson and to Ray Syn. 43, n. 13 (Pl. **61** and Text-fig. 1). Schmitz (1889) considers *Polyides rotundus* (Gmel.) Grev. as the type of the genus while Silva (1952) cites *P. lumbricalis* Ag.

Agardh gave a full description of the generic characters of *Polyides* and inserted a paragraph stating how this genus differed from *Furcellaria*, but he was not so precise in dealing with the single species which he assigned to the genus. To this species he gave the name *Polyides lumbricalis*, the epithet being derived from Bauhin (1623). Agardh stated 'Nomen antiquissimum habitum bene indicans, restituimus'. Hudson also had used the same epithet, deriving it also from the same entity of Bauhin for his species *Fucus lumbricalis* Hudson (1762, p. 471), a synonym of *Furcellaria fastigiata* (L.) Lamouroux. Hudson's *Fucus lumbricalis* is one of a long list of synonyms quoted by Agardh, and some of which are now known to belong to *Polyides* and some to *Furcellaria*. In addition, Agardh's *Polyides lumbricalis* var. *β fastigiatus* is based on *Fucus fastigiatus* L. which is here shown to be the type of *Furcellaria fastigiata* (Pl. **62**). Moreover, by the remark quoted above, Agardh obviously realized that other names were in use for the species he was describing. For all these reasons, the binomial *Polyides lumbricalis* should be considered illegitimate.

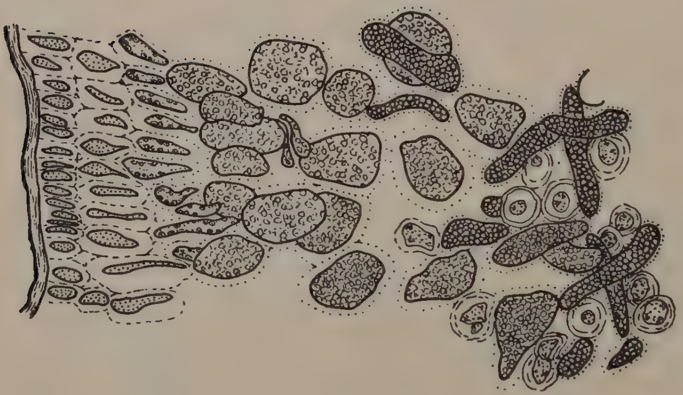
The earliest description of the single species of *Polyides* has usually been considered to be that of *Fucus rotundus* Gmelin (1768), listed by Agardh as a synonym of his *Polyides lumbricalis*. However, to quote Papenfuss (1950, p. 194), 'Gmelin did not describe this species as new but misidentified it with *Fucus rotundus* Hudson (1762, p. 471)'. The plant figured by Gmelin was *Polyides* and whether he mis-identified his material depends on the identity of *Fucus rotundus* Hudson. In the next section, this will be shown to be *Polyides* also. Gmelin was correct therefore in naming his plant *Fucus rotundus*.

Papenfuss (1950, p. 185) has considered *F. rotundus* Hudson to be the type of the genus *Bifurcaria* Stackhouse, and has made the combination *B. rotunda* (Hudson) Papenfuss and, since *Fucus rotundus* Hudson is *Polyides*, *Bifurcaria tuberculata* (Huds.) Stackhouse must be considered a synonym of *Polyides rotundus* (Huds.) Grev., as is



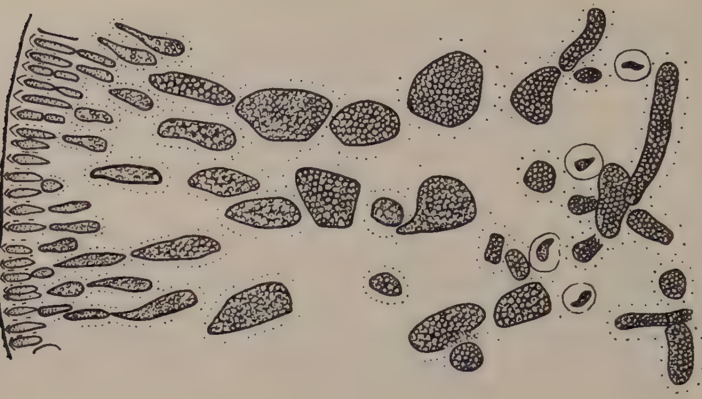
1

Text-fig. 1. Ray's Fucus kali geniculato similis. T.S. of specimen of Pl. **61** *c*. ×130.



2

Text-fig. 2. *Fucus fastigiatus* L. T.S. of specimen of Pl. **62** *a*. ×130.



3

Text-fig. 3. *Fucus caprinus* Gunnerus. T.S. of specimen of Pl. **63**. ×130.

shown by Ross in the next article (pp. 753–4). Papenfuss continues his account by stating: 'The plant that has passed under the name of *Polyides rotundus* (Gmelin) Greville should thus apparently be known as *Polyides caprinus* (Gunnerus) Papenfuss comb.nov. (=*Fucus caprinus* Gunnerus 1766, p. 96).' In a later section, it will be shown that *Fucus caprinus* Gunnerus is a synonym of *Furcellaria fastigiata* (L.) Lamour. and not of *Polyides rotundus* (Huds.) Grev.

The type species of *Polyides* is therefore *P. rotundus* (Hudson) Greville and its synonyms are:

Fucus rotundus Hudson, 1762, p. 471.
F. tuberculatus Hudson, 1778, p. 588.
F. radiatus Goodenough & Woodward, 1797, p. 202.
Polyides lumbricalis Agardh, 1822, p. 392.
Spongiocarpus rotundus (Gmelin) Greville, 1824, p. 286.
Polyides rotundus (Gmelin) Greville, 1830, p. 70.
Fastigiaria rotunda (Gmelin) Stackhouse, 1809, p. 91.
Bifurcaria tuberculata (Hudson) Stackhouse, 1809, p. 90.
B. rotunda (Hudson) Papenfuss, 1950, p. 185.

The type specimen of Fucus rotundus *Hudson*

The following is the description of *F. rotundus* given by Hudson (1762, p. 471):

> 24. *rotundus*. Fucus teres subdichotomus uniformis, ramis obtusis verucosis.
> Fucus kali geniculato similis, non tamen geniculatus. R. Syn. 43. Anglis, round Fucus.
> Habitat in rupibus marinis prope S. Ives in Cornubia. R. Syn.

Hudson does not provide an illustration of this species and no specimen of Hudson's of *Fucus rotundus* has been found, and without further information the identity of this species would remain doubtful. From the description, it seems likely that Hudson had no material of his own but was basing his description on Ray's (1724) earlier one. This is also suggested by the fact that, as already pointed out by Papenfuss (1950, pp. 184–5), Hudson gave this same plant of Ray's as a synonym of a new species *F. tuberculatus* in the second edition of the *Flora Anglica* (1778, p. 588) at the same time dropping the name *F. rotundus*. In the absence of a Hudson specimen of *F. rotundus*, it seemed best to look for the Ray specimen and to consider that plant the type specimen of *F. rotundus* Hudson. No. 1906, in the Sherardian Herbarium at Oxford, appears to carry the authentic Ray specimens (Pl. **61**; Text-fig. 1).

There are two specimens mounted at the top of the sheet, and the label is at the bottom, and so in order to show the specimens at natural size, it has been necessary to photograph them separately and to rearrange their relative positions. The specimen to the left at the top of the sheet (Pl. **61***c*) has been sectioned, and in consequence it seems best to designate this one as the holotype. As the axes are still cylindrical, it would seem that the specimens must have been dried without the application of pressure. This is shown quite clearly in Pl. **61***a*, which also shows regeneration of the broken tips excellently. The reference on the label to Syn. II, 4, 15, is to the second edition of Ray's *Synopsis methodica Stirpium britannicarum* (1696), whereas Gmelin (1768) and Hudson (1762) refer to the third edition (1724).

The specimen was exceedingly hard to cut and, except in high grades of alcohol, sections swelled rapidly and became very distorted. Examination of only slightly swollen sections showed the typical *Polyides* structure, particularly a regularly packed outer cortex of three layers of small cells and the feebly curving rows of cells connecting the medulla and inner cortex. Text-fig. 1 is a drawing of a small sector of a section in which the cell walls are swollen to about the same extent as those of *Fucus fastigiatus* L. (Text-fig. 2) and *Fucus caprinus* Gunnerus (Text-fig. 3). The features distinguishing this section from those of the other two algae are the uniformity of the medullary cells, the more regular arrangement of the cells of the inner cortex and the shape and size of the two to three layers of small cells of the outer cortex.

No Hudson specimen labelled *Fucus tuberculatus* is known, but Hudson's observations under this name are clearly based on the brown alga commonly known as *Bifurcaria tuberculata* (Huds.) Stackh. Nevertheless, Hudson cites *Fucus kali*...of Ray, the type of his earlier *F. rotundus*, under *F. tuberculatus*; hence his later name is illegitimate because superfluous, and it must be typified by Ray's plant. The implications of this for the nomenclature of the brown alga are discussed subsequently by Ross (see pp. 753–4).

B. *The genus* Furcellaria

Furcellaria Lamouroux, 1813 (syn. *Fastigiaria* Stackhouse, 1809)

Lamouroux (1813) included two species in *Furcellaria* when he erected this genus, *F. lumbricalis* (=*Fucus lumbricalis* var. alpha Turner) and *F. fastigiata* (=*Fucus lumbricalis* var. beta Turner). Neither species was designated the type of the genus by Lamouroux. In 1829 (p. 66) De la Pylaie named *Fucus lumbricalis* Gmelin as the type species and later Schmitz (1889) typified the genus with *Furcellaria fastigiata* (Huds.) Lamour. More recently, Papenfuss (1950, p. 194) has considered *Fastigaria Linnaei* as the type of Stackhouse's genus, against which *Furcellaria* is conserved.

Considering these three typifications in order, the first description of *F. lumbricalis* is given by Hudson (1762, p. 471), and a specimen of Hudson's bearing this name in the possession of the British Museum (Natural History) is clearly *Furcellaria* as is shown by the typical fibrous basal region of attachment. Figures given by Gmelin (1768) and Turner (1808) represent *Furcellaria*. In addition, Hudson, Gmelin and Turner all refer to a figure in Morison's *Historiae Universalis Oxoniensis* (1699, p. 648, 15, t. 9, f. 4) which represents *Furcellaria*. The identity of *Fucus lumbricalis* is not in doubt therefore and is clearly *Furcellaria*.

The identity of *Fucus fastigiatus*, on the other hand, has not previously been clearly established. The first description of a plant to which this name was attached is that given by Linnaeus in the first edition of the *Species Plantarum* (1753, p. 1162), and Hudson listed a *F. fastigiatus* in both the first (1762, p. 467) and second editions (1778, p. 588) of the *Flora Anglica*. Hudson clearly based his species of that name on Linnaeus's. Turner, however, not only had difficulty in identifying Linnaeus's *F. fastigiatus* with typical specimens of either *F. rotundus*[1] Gmelin or *F. lumbricalis* Hudson, but he did not consider that the Linnaean herbarium specimens all belonged to the same species. In 1802 (p. 315), he points out that 'From Linnaeus' collection is apparent what otherwise probably never would have been suspected, that what he really intended for his *F. fastigiatus* in the Species Plantarum is the same as the third variety of *Fucus rotundus* above mentioned', i.e. *F. rotundus* γ *fastigiatus*. At the same time as Turner lists the Linnaean herbarium specimen under this variety of *F. rotundus* he lists *F. fastigiatus* L. as a synonym of his *F. lumbricalis* β *fastigiatus* (1802, 1808). Turner's variety *fastigiatus* of *F. lumbricalis* Hudson, the second species of Lamouroux, thus appears to rest ultimately on the Linnaean description of *F. fastigiatus*. *F. fastigiatus* L. is therefore the type of *Furcellaria fastigiata* of Lamouroux and, as will be shown, the Linnaean specimen selected as the type, the one Turner made the basis of his variety γ *fastigiatus* of *Fucus rotundus*, has the structure of *Furcellaria*.

The first species listed by Stackhouse (1809, p. 90) in his genus *Fastigiaria* is *F. Linnaei*, the one considered the type by Papenfuss (1950). From Stackhouse's references, this is clearly a synonym of and based on *Fucus fastigiatus* L.

F. lumbricalis Hudson and *F. fastigiatus* L. are therefore both representative of *Furcellaria* and are the respective types of the two species listed by Lamouroux when he erected the genus. The question whether they represent one or two taxa is not one within the scope of the present paper. In modern times, the reduced forms of the Baltic, of which the type specimen is probably one, have not been considered to represent a separate species. The earlier writers kept them distinct, although a search of herbaria might show that English botanists of that period misidentified other algae with the Baltic form of *Fucus fastigiatus*. Therefore, until it has been shown that there is more than one species of *Furcellaria*, *Fucus fastigiatus* L. must be considered the type of the genus as it has priority over *F. lumbricalis* Hudson.

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[1] Turner (1802, 1808) excludes Hudson's *F. rotundus* and Ray's plant to which Hudson refers from the synonymy of Gmelin's *Fucus rotundus*.

Mention should be made of two other synonyms of *F. fastigiatus* L.:

1. *Fucus furcellatus* L.

Although the specimen bearing this name in the Linnaean herbarium is a brown alga, Linnaeus (1763, p. 1631) considered it to be closely related to *F. fastigiatus* for he states '*F. fastigiato* proxime accedit, sed altior, ramis crassioribus apice acuminatis'. This discrepancy between specimen and description was noted by Turner (1802, p. 323). In addition, Linnaeus refers to a figure of Morison's (f. 15, t. 9, f. 4) which is clearly *Furcellaria fastigiata*. Gunnerus (1768, p. 82) considered that his *Fucus caprinus* was identical with *F. furcellatus* L., and judging from an entry in Linnaeus's handwriting in his own copy of the second edition of the *Species Plantarum*, Linnaeus thought the same. Hudson had described *F. lumbricalis* in 1762 and had also referred to the same figure of Morison's as referred to by Linnaeus. On the basis of the description, *F. furcellatus* is a synonym of *F. lumbricalis* Hudson, but not on the evidence of the specimen in the Linnaean herbarium. Although Hudson changed the name of his *F. lumbricalis* to *F. furcellatus* in the second edition of the *Flora Anglica*, making it synonymous with Linnaeus's plant of the same name, this does not alter the fact that *F. lumbricalis* Hudson was validly and effectively published before *F. furcellatus* and based on *Furcellaria*.

2. *Fucus caprinus* Gunnerus

This species has been cited by different workers as a synonym of both *Furcellaria fastigiata* (L.) Lamour. and of *Polyides rotundus* (Huds.) Grev., and more recently Papenfuss (1950, pp. 184, 185 and 194), having equated Hudson's *Fucus rotundus* with Withering's *F. bifurcatus*, made Gunnerus' plant *F. caprinus* the type of *Polyides*. A photograph of the type specimen, kindly lent by Dr O. Gjaerevoll of Trondheim, is reproduced in Pl. **63**. This is certainly the specimen figured by Gunnerus in 1768 as fig. 4, although it appears there as a single specimen, whereas now there are two pieces, probably due to an accidental break. The specimen is sterile and is without the basal region. This specimen has been sectioned and the similarity of its structure (Text-fig. 3) to that of *F. fastigiatus* L. is quite striking. *F. caprinus* Gunnerus is therefore a synonym of *F. fastigiatus* L. Kjellman (1883, p. 152) considered *F. caprinus* Gunnerus to be f. *tenuior* of *Furcellaria fastigiata*.

The correct name for the type species of *Furcellaria* is therefore *F. fastigiata* (L.) Lamouroux and the synonyms are:

Fucus fastigiatus Linnaeus, 1753, p. 1162.
F. lumbricalis Hudson, 1762, p. 471.
? *F. furcellatus* Linnaeus, 1763, p. 1631. (On the basis of the description and the reference to the Morison figure but not the herbarium specimen.)
F. caprinus Gunnerus, 1766, p. 96.
F. rotundus Gmelin γ *fastigiatus* Turner, 1802, p. 310; 1808, pp. 11, 12.
Furcellaria lumbricalis (Turner) Lamouroux, 1813, p. 46.
F. fastigiata (Turner) Lamouroux, 1813, p. 46.
F. fastigiata (Hudson) Lamouroux, Schmitz, 1889, p. 454.
Polyides lumbricalis Ag. β *fastigiata* (L.) C. Agardh, 1822, p. 393.
P. caprinus (Gunnerus) Papenfuss, 1950, p. 194.
Fastigiaria Linnaei Stackhouse, 1809, p. 90.
F. lumbricalis (Gmelin) Stackhouse, 1809, p. 91.
? *F. furcellata* (Hudson) Stackhouse, 1809, p. 91.

The type specimen of Fucus fastigiatus *L.*

Linnaeus (1753, p. 1162) describes *Fucus fastigiatus* as follows:

> 25. *fastigiatus.* Fucus dichotomus ramosissimus teres uniformis fastigiatus. *It. oel.* 120. *Fl. suec.* 1008.
>
> Fucus caule lineari dichotomo *Roy. lugdb.* 514. Fucus palmaris tenuis in orbem expansus in segmenta bifida breviora teretia divisus. *Moris. hist.* 3. p. 649, f. 15, t. 9, f. 9. Fucus marinus polyschides. *Loes. pruss.* 77, t. 15. *Habitus in Oceano* Balthico.

In the Linnaean herbarium, in the keeping of The Linnean Society of London, there are four sheets of specimens under this name. The specimens on sheets three and four appear to belong to the Fucales and have therefore not been considered. Of the four specimens on the top sheet (Pl. **62**), the one nearest the top of the sheet (Pl. **62***a*) is rather shrivelled, has no attachment organ but is repeatedly dichotomously branched. The remaining three specimens (Pl. **62***b*) resemble *Ahnfeltia plicata* to a certain degree but may belong to the same taxon as the top specimen. The specimens on sheet 2 resemble these. Since Dawson Turner's opinion about these specimens added to the confusion existing between forms of what we now call *Furcellaria* and *Polyides*, it is well to quote his notes about them: '4 papers. *one* contains four specms, the one at the top *F. rotundus* γ 3 below are *F. plicatus*—the second paper from König is *F. plicatus* β—the 3rd and 4th are a *Fucus* quite new to me (mem? *to correct* a *mistake* about this *plant* in Syn. Fuc.).' It is not clear by reading Turner's 1802 and 1808 publications what mistake he meant to correct.

The uppermost specimen, the one considered to be *Fucus rotundus* γ by Dawson Turner, has been selected as the holotype (Pl. **62***a*), and a section (Text-fig. 2) shows that it has the structure of *Furcellaria* and not *Polyides*. The section, which was mounted in Schultz's solution, shows an outermost single layer consisting of closely and regularly packed slightly elongated cells. The cells of the succeeding layers are less regularly and less closely arranged as well as larger and they form a transition zone to the large cells of the inner cortex. The cells of the inner cortex are irregular in shape and among the innermost are some which are elongated in the plane of the section, becoming more numerous towards the medulla, the secondary hyphal filaments. In the medulla, appear the cells of the primary medullary filaments, small in diameter, with a narrow lumen and thick walls. Grains of Floridean starch are abundant in the cells of the inner cortex and the cells of the secondary hyphal filaments.

The type specimen of *Fucus fastigiatus* L. is far from being a typical specimen of *Furcellaria fastigiata* (L.) Lamour. and, without knowledge of the information provided by a section, those familiar only with the usual form found on the Atlantic shores might well be excused for being uncertain of its identity. Neither is it surprising that the older writers considered that the larger forms belonged to another species, either *Fucus lumbricalis* Hudson or *F. furcellatus* L. In the description, Linnaeus gives the Baltic as the locality for *F. fastigiatus* L., but there is no information as to where the specimens in the Linnaean herbarium were collected. Waern (1952, p. 188), who has written at length about the nomenclatural tangles surrounding *Furcellaria fastigiata*, considers the specimen now selected as the type (Pl. **62***a*) to be 'like an old piece of *Furcellaria fastigiata*, which may be found dropped on the roads of Gotland', i.e. what is known in those parts as Kräkel. Comparison of the specimen of Pl. **62** and photographs of Baltic specimens of *F. fastigiata* given by Waern (1952) certainly support this statement. Herbarium specimens of material from the Baltic loaned by Dr M. Waern also stress this similarity. Some of Dr Waern's Baltic specimens are also similar in appearance to the other Linnaean specimens (Pl. **62***b*).

Conclusions and summary

The generic characters, such as were recognizable to botanists of that time, of *Polyides* and *Furcellaria* were clearly stated at the time these genera were erected. The earliest validly and effectively published description of each of the single species of these two genera, checked by reference to herbarium specimens, has been established, and in consequence the correct binomial for each type species established. They are *Polyides rotundus* (Hudson) Greville and *Furcellaria fastigiata* (L.) Lamouroux. *Fucus caprinus* Gunnerus has been shown to be *Furcellaria* and not *Polyides*, and hence it is a synonym of *Furcellaria fastigiata* (L.) Lamour. Since *Fucus rotundus* Hudson has been shown to be *Polyides* and not *Bifurcaria*, a new combination has to be made for *Bifurcaria rotunda* (Hudson) Papenfuss.

Acknowledgements

This search through the old records and herbaria has been greatly assisted by help from many people to whom I offer my thanks: N. Y. Sandwith, Esq., Hon. Curator of the Linnaean herbarium; Dr E. F. Warburg, Keeper of the herbarium at the University of Oxford; Dr O. Gjaerevoll, of the Kgl. Norske Videnskabers Selskab Museet, Trondheim; Miss C. I. Dickinson, of the herbarium of the Royal Botanic Gardens, Kew; Mr R. Ross, Mrs L. Irvine and Miss Y. Chamberlain of the British Museum (Natural History); and Dr M. Waern of Uppsala. I am also indebted to Mr E. Ashby for the photographs of Pls. **61** and **63**, and to the University of Manchester for a grant from the Lang Fund towards the cost of their reproduction.

Sections of the three specimens have been lodged with the respective specimens. The negatives of the photographs of Pls. **61–63**, the catalogue numbers of which are given, are in the Department of Cryptogamic Botany, the University of Manchester.

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EXPLANATION OF PLATES

Plate **61**. Fucus kali geniculato similis, non tamen geniculatus Ray. Herb. Sherard No. 1906

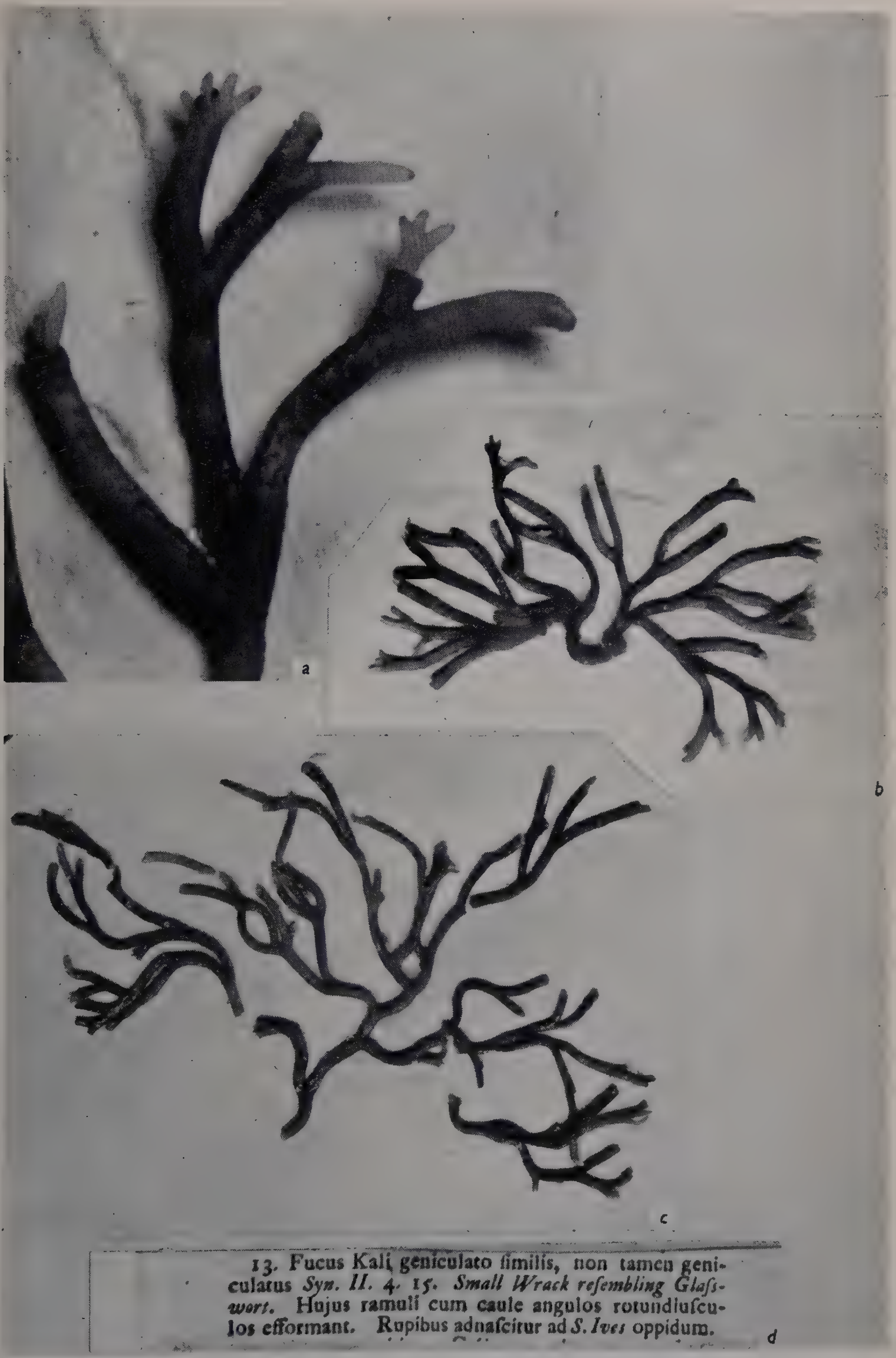
(*a*) Tips of some branches of specimen of fig. 6 showing regeneration. Neg. Fuc. | Kal | 1956 | 3. × 4.
(*b*) R.H. specimen on herbarium sheet. Neg. Fuc. | Kal | 1956 | 3. × 1.
(*c*) L.H. specimen on herbarium sheet, the one sectioned, now designated the holotype. Neg. Fuc. | Kal | 1956 | 2. × 1.
(*d*) Label on sheet. Neg. Fuc. | Kal | 1956 | 1. × 1.

Plate **62**. *Fucus fastigiatus* Linnaeus. (All Neg. Fuc. | fas | 1957 | 1.)

(*a*) Upper specimen on herbarium sheet, the one considered *Fucus rotundus γ fastigiatus* by D. Turner, the specimen sectioned and now designated the holotype. × 1.
(*b*) Lower specimens on same herbarium sheet with D. Turner's identification pencilled in. × 1.
(*c*) The number and label of the herbarium sheet. × 1.

Plate **63**. *Fucus caprinus* Gunnerus. (Neg. Fuc. | cap | 1954 | 1.)

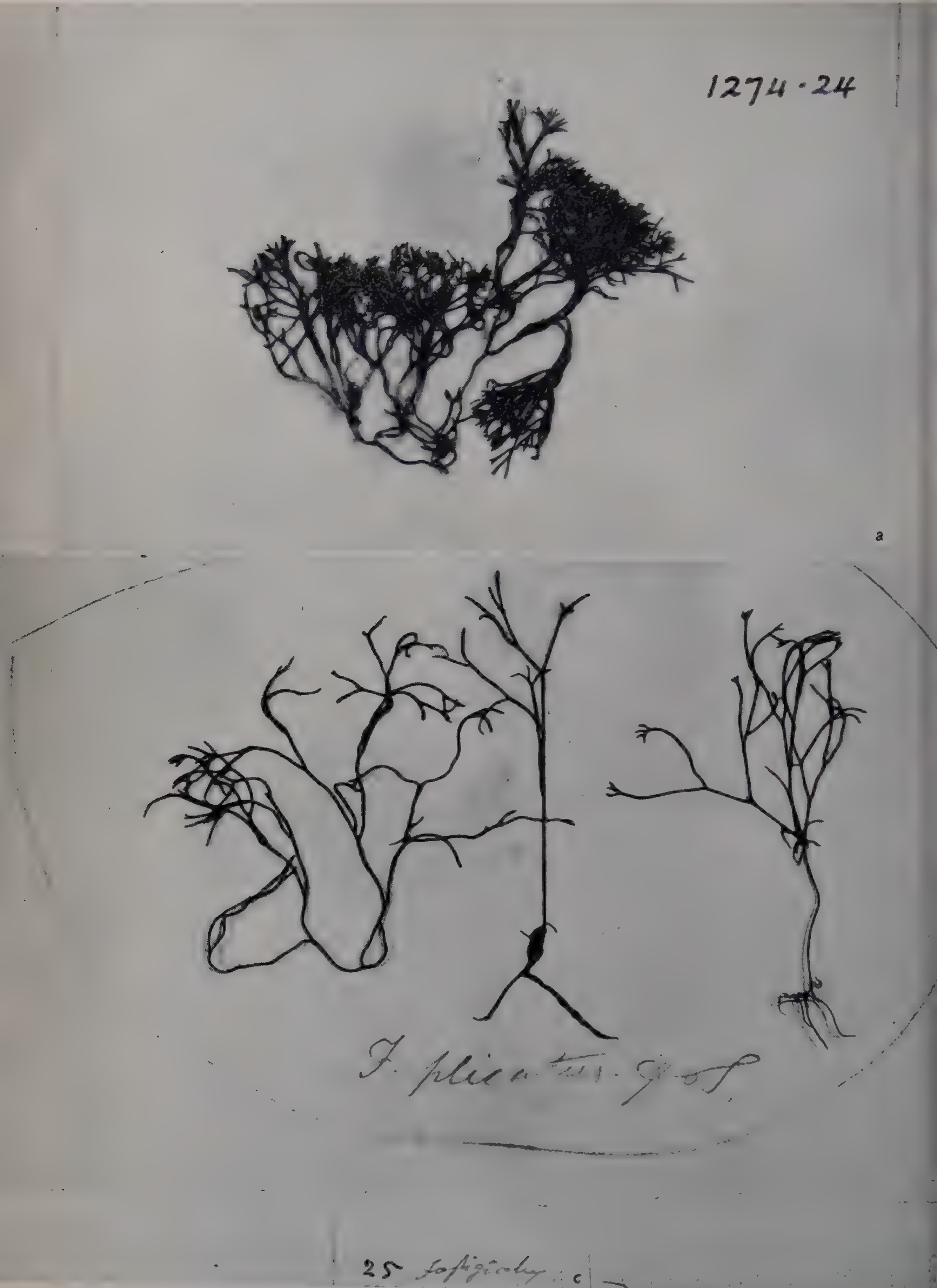
(*a*) Specimen. × $\frac{1}{2}$.
(*b*) Label on herbarium sheet.



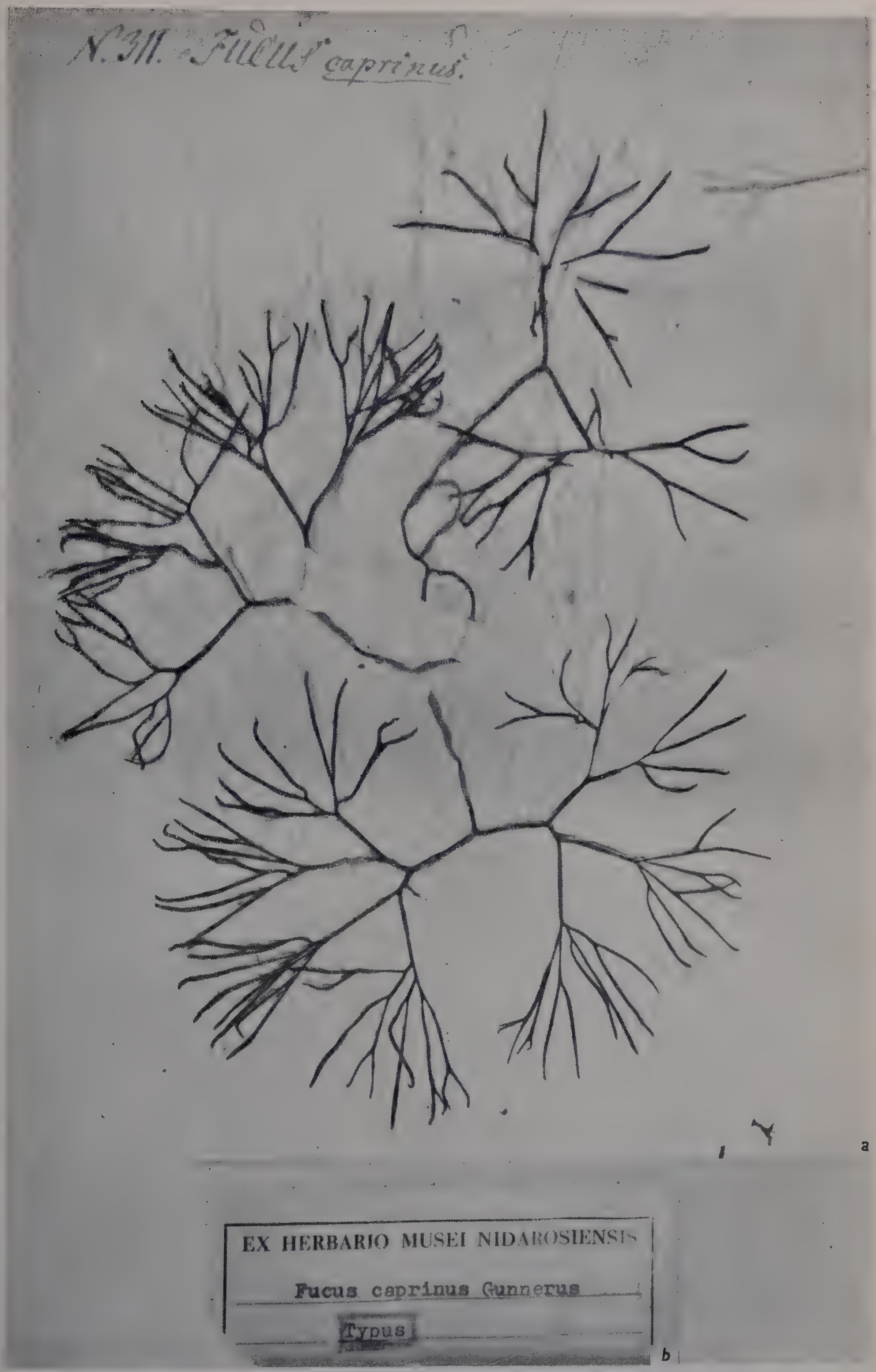
13. Fucus Kali geniculato ſimilis, non tamen geniculatus *Syn. II. 4. 15. Small Wrack reſembling Glaſswort.* Hujus ramuli cum caule angulos rotundiuſculos efformant. Rupibus adnaſcitur ad *S. Ives* oppidum.

Fucus rotundus Huds. Type specimen in Herb. Sherard, Oxford.

(*Facing p.* 752)



Fucus fastigiatus L. Specimens in Linnaean Herbarium.



Fucus caprinus Gunnerus. Type specimen in Trondheim Museum Herbarium.

The Type Species of Bifurcaria Stackhouse. By R. Ross, British Museum (Natural History).

[Read 7 November 1957]

Drew, in the contribution which immediately precedes this, has demonstrated that *Fucus rotundus* Huds. is the red alga which is the sole species of the genus *Polyides* Ag. As Papenfuss (1950, pp. 184–5) has recently stated that this species is the type of the genus *Bifurcaria* Stackh., normally placed in the brown algae, it is necessary to examine the consequences on the application of that name of this finding of Drew's. Papenfuss's statement was based on the assumption that *Fucus rotundus* Huds. was the brown alga described in standard works as *Bifurcaria tuberculata* (Huds.) Stackh. (cf. De Toni, 1895; Newton, 1931; Hamel, 1931–9). As this is the only brown alga which there will be occasion to consider in this discussion, it will be convenient, in order to avoid begging the question of its correct name, to refer to it simply as the brown alga.

The first description of the brown alga seems to have been that published by Hudson (1778, p. 588) under the name *Fucus tuberculatus*. This reads:

> *tuberculatus* 52. FUCUS fronde filiformi subdichotoma, ramis obtusis tuberculatis.
> Fucus kali geniculato similis, non tamen geniculatis. *R. syn. 43*
> *Anglis*, tuberculated Fucus.
> Habitat *in rupis et saxis submarinis prope* St. Ives *in* Cornubia. ♃. VI–X.
> Obs. *affinis F. fastigiato, sed differt non uniformiter dichotomus nec fastigiatus sed ramis inaequalibus, ultimis fructificationibus tuberculatis aspersis.*

A comparison of this with the account of *F. rotundus* in his first edition (Hudson, 1762, p. 471), quoted by Drew above (p. 747), leaves little doubt that Hudson based that account on Ray's description and specimen, but that before his second edition he saw a specimen of the brown alga, which he, erroneously, identified with Ray's plant. Both the word 'tuberculatis' in the diagnosis, substituted for 'verrucosis' of ed. 1, and the observation are clearly based on the brown alga, and it was presumably the characters of this plant which made him consider that a change of epithet was desirable. Since Hudson quoted the 'Fucus kali...' of Ray, which is the type of *F. rotundus* Huds., as a synonym of his *F. tuberculatus*, that name is illegitimate because superfluous when published, and must be typified by the Ray plant, i.e. *Polyides rotundus* (Huds.) Grev. *Fucus tuberculatus* Huds. is illegitimate on a second ground also: it is a later homonym of *F. tuberculatus* Lightf. (1777, p. 926).

The next description of the brown alga is that under the name *F. bifurcatus* Velley in Withering (1792, p. 257). In the diagnosis of this Withering gives first an English translation of Hudson's diagnosis of *F. tuberculatus*, followed by further diagnostic characters supplied by Velley and himself. In the observations which follow he also gives first an English translation of the observations in Hudson's account of his *F. tuberculatus*, and he follows this with a long description by Velley based on an examination of fresh material. This concludes: 'Mr Hudson has named this plant *F. tuberculatus*, but as several other Fuci put on tuberculated appearances in maturity, I have in conformity to its character, and mode of growth, called it *F. bifurcatus*.' There is no reference anywhere to the 'Fucus kali...' of Ray nor to *F. rotundus* Huds. It is quite clear, not only from the description but also from the figure (Withering, 1792, pl. 17, fig. 1), that the plant to which Velley was applying the name *F. bifurcatus* was the brown alga. Mr Peter Dixon has examined his specimen, no. 210 in vol. 5 of his herbarium in the Liverpool Public Museum, and confirms that this is so. There is the question, however, of whether Art. 7, Note 4, of the Code (Lanjouw (ed.), 1956) applies to this case; if it does, Ray's plant is the type of *F. bifurcatus* as well as of *F. tuberculatus* Huds. However, of the two elements included by Hudson in his *F. tuberculatus*, the account in Withering mentions only one, the Hudson specimen, and does not refer to the other, the Ray synonym and specimen, which is the type. We may therefore hold, I consider, that *F. bifurcatus* Velley in Withering is a new species, in the synonymy of which Velley included *F. tuberculatus* Huds. [pro parte, excl. parte typ., syn. Raii]. Its type is thus Velley's specimen, and we avoid the absurdity of typifying a species by a specimen which does not agree with the original diagnosis and description, and which is nowhere mentioned or directly referred to in the original account.

Stackhouse's (1809, p. 59) original diagnosis of *Bifurcaria* reads: 'Fr.[ons] caulis nudus teres; apices dichotomi, angulis rotundiusculis: maturitate tumidis: mucus reticulosus, cum seminum orbiculis, et papillis in cute foraminosis.*** *** Vid. Eng. Bot. 726 et delineationem.' He includes (*loc. cit.* p. 90) one species only, *B. tuberculata,* of which his account reads thus: 'Fr.[ons] dichotomiae angulis curvatis; apicibus furcatis, longis, fructificatione diaphanis. Icones. Esp. t. 121. With. t. 17, f. 1. Eng. Bot. t. 726. App. Descr. L. Tr. III. 198. Ray Syn. 43. n. 13.' The three figures are all of the brown alga; Esper's (1802, t. 121) and Smith & Sowerby's (1800, t. 726) are both named *Fucus tuberculatus* and are accompanied by references to Hudson's publication of that name and also to the Ray synonym. Goodenough & Woodward's (1797, p. 198) description is also of the brown alga, and it too is under the name *F. tuberculatus*, Hudson's publication of which and the Ray synonym being cited. The reference to Ray is to 'Fucus kali...'. Stackhouse, it will be noted, does not himself cite Hudson's original publication of *F. tuberculatus* except indirectly, although he cites the *Flora Anglica* under many other species. He must, nevertheless, be held to be making by indirect reference a new combination under *Bifurcaria* for *Fucus tuberculatus* Huds. Hence the type of his *Bifurcaria tuberculata* is Ray's specimen, i.e. *Polyides rotundus* (Huds.) Grev. His diagnoses of the genus and the species, the three figures and one of the two descriptions he quotes are based, however, on the brown alga.

'The nomenclatural type...of a genus...is a species' (Lanjouw (ed.), 1956, Art. 9). The problem in the case of *Bifurcaria* is which species, *Polyides rotundus* or the brown alga. Both elements are included in Stackhouse's account of the genus, but it is clear that he used only the brown alga in drawing up his description of it, and his inclusion of *P. rotundus* in his account of *Bifurcaria tuberculata* was due to his following Hudson in erroneously identifying the brown alga with Ray's 'Fucus kali...'. Thus, although Ray's specimen is, as a result of this error, the type of *B. tuberculata* (Huds.) Stackh., which is accordingly a synonym of *Polyides rotundus* (Huds.) Grev., the type species of *Bifurcaria* Stackh. is the brown alga, of which, as we have seen, *Fucus bifurcatus* Velley in Withering is the earliest legitimate name. The correct name of the species is therefore:

Bifurcaria bifurcata (Velley) comb.nov.

Fucus bifurcatus Velley in Withering, *Bot. Arrang. Brit. Pl.*, ed. 2, **3**, 257 (1792).

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The cytogeography of the Bothriochloa ischaemum complex. Gramineae. I. Taxonomy, and Geographic Distribution. By R. P. Celarier and J. R. Harlan[1]

(With Table 1 and Map)

[Read 7 November 1957]

Many members of the grass tribe Andropogoneae have been known for some time to be of considerable potential for pasture and range improvement in the United States. Of the genera that have been studied, *Bothriochloa* and the closely related *Dichanthium* and *Capillipedium* are among those with forms agronomically important in the Southern Great Plains. These are poorly understood cytologically, morphologically, and taxonomically, yet they are of considerable importance in the Old World and of much promise for the New World. The species, *Bothriochloa ischaemum* (L.) Keng, is of special interest in the Southern Great Plains.

The objective of this study was to grow together, in an experimental garden, introduced samples (accessions) of *B. ischaemum* from throughout its geographical range of distribution, and to make both a cytological and morphological survey of them. The carrying out of this objective seemed to offer possibilities for drawing conclusions on the pattern of variation of the species, and also something about its origin and evolutionary mechanics.

Materials and methods

All materials used in this study were grown in an experimental garden at the Oklahoma Agricultural Experiment Station, and the details of their management have been explained elsewhere (Celarier, 1956).

There were fifty-seven samples of *B. ischaemum* present in the nursery, representing almost the entire range of distribution of the species. However, there is good reason to believe that seven of these came originally from a single introduction from Amoy, China, to the California Agricultural Experiment Station in 1917. This sample has a somewhat obscure history that has recently been summarized by Harlan (1952) and Celarier & Harlan (1955), and it now seems quite clear that both 'King Ranch Bluestem' and 'Texas Yellow Beardgrass' have been derived from this sample.

This introduction and selections from it have been grown extensively throughout the southern part of the United States during the past thirty-five years. Three of the samples studied apparently came from the material collected on King Ranch, Texas, and increased by the Soil Conservation Service in 1937 under the number T-3487. One sample, A-2559, was selected from 'Texas Yellow Beardgrass' which was grown soon after its introduction at the Angleton, Texas, Substation as T.S. 8413. The three remaining samples, A-3503, A-5639 and A-5636, were supplied by J. E. Smith of the Soil Conservation Nursery at San Antonio and came from plants that had escaped from cultivation in South Texas. In order to determine the variation, both cytological and morphological, that had accumulated in these samples during the 35 years they have been grown in this country, cytological and morphological data were taken for each sample.

Cytological studies were made exclusively from bud material fixed in Carnoy's fluid, stored in a refrigerator and studied as time permitted. Several plants were studied for nearly all samples.

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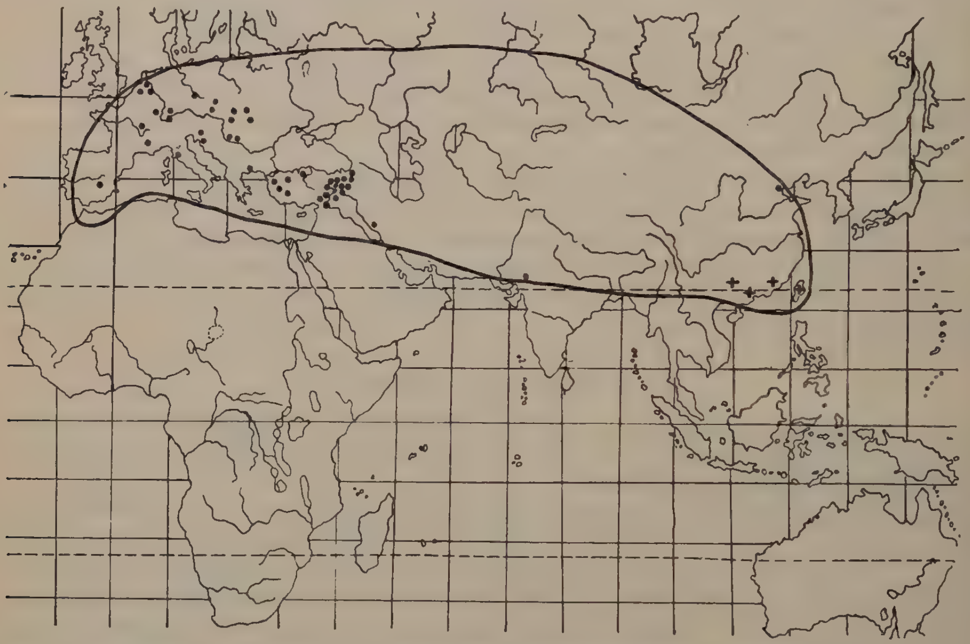
Morphological data were taken from ten plants of each sample, whenever possible. There was no selection of these plants except that the first ten of each row that produced flowers were used. Data were taken both in the field and from herbarium specimens, depending on the nature of the data. Specimens for all samples have been deposited in the Oklahoma State University Herbarium, and most samples also in the following herbaria: Royal Botanic Gardens Herbarium, Kew, England; University of Pretoria Herbarium, Pretoria, South Africa; Smithsonian Institution Herbarium, Washington, D.C.; Missouri Botanical Garden Herbarium, St Louis, Missouri; University of California Herbarium, Berkeley, California; the Tracy Herbarium, A. and M. College of Texas, College Station, Texas, and Southern Methodist University Herbarium, Dallas, Texas.



Map 1. Geographical distribution of *B. ischaemum* with locations of samples studied. —, general area of distribution of *B. ischaemum*; •, var. *ischaemum*; +, var. *songarica*.

GEOGRAPHIC DISTRIBUTION

The distribution of *B. ischaemum* is rather extensive throughout the subtropical and temperate regions of Eurasia. This species has been collected in the Atlas Mountains of North Africa (Battandier & Trabut, 1902; Maire, 1949) and it is rather common in eastern Spain (Willkomm & Lange, 1880), Italy (Fiori, 1929), France (Coste, 1906), Belgium, Germany, Czechoslovakia, Austria, Hungary, Romania, Yugoslavia (Hegi, 1936), Bulgaria, and Greece (Hayek, 1933). In Russia it is common in the European section, western Siberia and central Asia (Komarov, 1934). It also extends through Mongolia and northern China (Komarov, 1934; Keng, 1933). The northern limit for the species is about 53° latitude in Belgium and Germany and approximately 56° latitude in the Upper Dnieper section of Russia.

The species is found abundantly in the Caucasian Mountains (Grossheim, 1939), Turkey (Post, 1933), occasionally in Syria and Lebanon (Post, 1933), Iraq (present report), Iran (Komarov, 1934; Parsa, 1948–52), northern Afghanistan (Vavilov & Bukinich, 1929) and probably also in Pakistan. It has been reported from the Himalayas of northern India (Pampanini, 1913–14; Stewart, 1945; Collett, 1902; Komarov, 1934) and in eastern Turkistan (Komarov, 1934). The distribution of the species in China is not well known, but it probably is common in the southern part of the country (Hitchcock, 1929; Keng, 1933, 1930, 1936) and has been found as far north as Peking (Hackel, 1889; Keng, 1933).

Map 1 gives a general outline of the distribution of the species, as well as the localities of the samples used in this study.

TAXONOMY

Bothriochloa ischaemum is often included in the subgenus *Amphilophis* of the genus *Andropogon*. This subgenus was described by Trinius (1833), and was later adopted by Hackel (1889), Chase (1950) and many others. It was raised to generic rank by Nash (1901) and was called *Amphilophis*. Nash presented a more detailed description of the genus (1909), and described many species. This position and nomenclature was maintained by Stapf (1919) in his treatment of the African Gramineae, and by many other taxonomists, especially those working in Asia and Africa. However, Kuntze (1891), from a specimen of *Andropogon glaber* Roxb., had earlier described the group as a new genus, *Bothriochloa*. This species was originally described by Kuntze as *Bothriochloa anamitica*, but it was later shown by Camus (1930) to be the same as *Andropogon glaber* of Roxburgh. The generic name *Bothriochloa* is used by most present-day taxonomists working in the Old World tropics (Camus, 1930; C. E. Hubbard, 1934; Keng, 1939; Henrard, 1940), as well as a few workers in America (Herter, 1940; Cabrera, 1953).

The species *Andropogon ischaemum* was described by Linnaeus (1753) in the first edition of *Species Plantarum*, and in the fourth edition of this work Willdenow (1805) enlarged the description, giving considerably more details concerning the floral parts. He pointed out that the glumes, especially near the base, were quite hairy.

The next major treatment of the species was in Hackel's (1889) monograph. Two features of this study make it extremely valuable: first, a very detailed description of the species was written from direct observation of living plants; and secondly, a very large amount of herbarium material was studied.

In this work Hackel recognized six varieties. One of these, var. *radicans*, had been previously considered to be a distinct species, *Andropogon radicans* Lam., and most present-day workers have continued to regard it as such (Stapf, 1919; Camus, 1930). Of the remaining five varieties only one, var. *ischaemum* (*genuinus*), had completely glabrous nodes. The other four are differentiated from one another principally by the length of nodal hairs and leaf pubescence.

A detailed morphological analysis was made of each of the fifty-seven samples grown under fairly uniform conditions. Data were tabulated for the following characters: pubescence of leaf, ligule, and node; ratio of length of leaf to maximum width; height (or length) of stem; general growth habit; susceptibility to foliage diseases; ratio of length of the lowest raceme to that of the primary axis of the inflorescence; degree of second-order branching of the lower racemes; size relationship of the sessile and pedicellate spikelets; the amount and location of hairs on the spikelets; degree and frequency of depression on the back of the first glume; general shape and pubescence of the lower lemma; number of nerves in first glume of the sessile spikelet; ratio of length of awn to length of spikelet; and time of flowering.

Considerable variation occurred in most of the characters considered. For the most part, this variation was found both within and between entries and appeared to have little association with reproductive isolation.

However, two rather distinct morphological types were found, which are correlated with geographical distribution and chromosome number, and are, from these studies, considered as distinct varieties.

Bothriochloa ischaemum var. *ischaemum*

Andropogon ischaemum L. var. *genuinus* Hack. (1889). In De Candolle, *Monogr. Phaner.* **6**, 475.

Tufted perennial. Stems slender, erect, simple to much-branched at maturity, 30–50 in. tall; nodes glabrous or very minutely pubescent. Leaves glabrous or with a few scattered hairs on the upper surface, linear, with a variable length-width ratio whose means range from 34·2 to 70·2, with a ligule 1 mm. or less. Inflorescence somewhat digitate, primary axis essentially glabrous, shorter than racemes, with the ratio of the length of lowest raceme to length of primary axis greater than two (range of means is from 2·2 to 6·2); second-order branching of racemes infrequent, and no greater degree of branching seen. Sessile spikelets oblong or somewhat elliptic; callus densely bearded with hairs. Glumes membranous; lower glume 5–9-nerved, back lightly long-haired on lower half, usually round but occasionally with a slight dimpling. Lower lemma oblong to obtuse, usually sparsely ciliate, occasionally glabrous. Upper lemma stipiform and awned; the ratio of the awn length to that of the spikelet is less than 3·6. Anthers three. Pedicellate spikelet subequal to the sessile, glabrous or occasionally a few short hairs, smooth on the back.

The $2n$ chromosome number is 40 in most samples, although two samples with $2n=60$ have been found. All samples so far studied have been found immune to the foliage diseases present in our nursery. It is distributed throughout Europe, parts of Middle Asia, and occasionally in the Far East.

Typical form (Typus Reichb. 651, Schultz 181) is represented in this study by the following collections of the senior author. *Spain*: Madrid (A-4439); *Italy*: Pisa (A-4011); *France*: Grenoble (A-3959), Pont de l'Arc (A-4008), Strasbourg (A-4007), Bas Rhin (A-5730), Paris (A-3794), specific origin unknown (A-5731); *Belgium*: Brussels (A-3240), Antwerp (A-3701), Bommershoven (A-3902); *Germany*: Wehrda (A-3705); *Austria*: Vienna (A-3955); *Czechoslovakia*: Bohemia (A-4251), Slovakia (A-4252), West Kosice (A-4250); *Hungary*: Budapest (A-4798), Szentes (A-5422); *Yugoslavia*: Ljubljana (A-4801 and A-4777), Zemun (A-4803), Belgrade (A-4802); *Greece*: Eastern Macedonia (A-4776); *Turkey*: Eskişehir (A-565 and A-564), Zonguldak (A-1366), Kastamonu (A-1367), Tunkeli (A-3457), Sinop (A-2553), Kayseri (A-3465), Malatya (A-563), Elâziz (A-1341), Bingal (A-562), Erzincan (A-567), Trabzon (A-1365), Coruh (A-1369 and A-1368[1]), Kars (A-1358), Mus (A-561), Mardin (A-1343), Van (A-1360), Hakkari (A-560), Maras (A-1359[1]); *Iraq*: Baghdad (A-3699); *India*: Punjab (A-3057); *China*: Peking (A-5704), specific origin unknown (A-5637); *North America*: Arizona, introduced (A-4092).

Bothriochloa ischaemum Keng. var. *songarica* (Rupr.) Celarier & Harlan, comb.nov.

Andropogon ischaemum L. *β songaricus* Rupr. (1841). In Fischer & Meyer, *Enum. Plant.* a cl. Schrenk *lect.* **1**, 2.

Similar to var. *ischaemum* with the following exceptions. Plants decumbent in general growth habit, somewhat more robust, 40–60 or more inches tall; nodes with a distinct ring of hairs. Leaves much more hairy, especially near the ligule, and underside of the leaf often pubescent. Primary axis of the inflorescence longer, with the ratio of lower racemes to the axis between 1·0 and 2·0; second-order branching of the racemes common and tertiary branching frequent. Lower glume of sessile spikelets seldom smooth on the back, usually with slight dimpling to strong dishing, but never pitted. The mean awn/spikelet ratio is greater than 3·6. Lower glume of the pedicellate spikelet often with long hairs on lower half of back and with occasional dimpling or dishing.

The $2n$ chromosome number is 50 or 60, and all samples studied have been found susceptible to foliage diseases, especially leaf rust. The differentiation of these varieties is shown in Table 1.

[1] These samples are $2n=60$.

Table 1. *Characteristics of* B. ischaemum *var.* ischaemum *and* songarica[1]

Samples examined	Origin, Far East	Ratio: raceme/axis	Node pubescent	Leaf pubescent	Leaf disease susceptible	Growth habit	Ratio: awn/spikelet	Chromosome no.		
								40	50	60
			var. *ischaemum*							
45 (in total)	0	> 2·0	0	0	0	Erect	< 3·6	×	.	.
A-5637	×	> 2·0	0	0	0	Erect	< 3·6	×	.	.
A-5704	×	> 2·0	0	×	0	Erect	< 3·6	×	.	.
A-1368	0	> 2·0	0	0	0	Erect	< 3·6	.	.	×
A-1359	0	> 2·0	0	0	0	Erect	3·8–4·8	.	.	×
			var. *songarica*							
A-1347	×	> 2·0	×	×	×	Decumbent	3·8–4·8	.	.	×
A-5638	×	> 2·0	×	×	×	Decumbent	3·8–4·8	.	.	×
A-5636	×	1·0–2·0	×	×	×	Decumbent	3·8–4·8	.	.	×
A-2582	×	1·0–2·0	×	×	×	Decumbent	3·8–4·8	.	.	×
A-726	×	1·0–2·0	×	×	×	Decumbent	3·8–4·8	.	×	.
A-2559	×	1·0–2·0	×	×	×	Decumbent	3·8–4·8	.	×	.
A-5635	×	1·0–2·0	×	×	×	Decumbent	3·8–4·8	.	×	.
A-5639	×	1·0–2·0	×	×	×	Decumbent	3·8–4·8	.	×	.

[1] In the table the × indicates that the entry is as described, the 0 indicates that it is otherwise. Whenever possible the specific deviation is given.

It is not clear to the authors exactly where two of Hackel's varieties, *fallax* and *laevifolius*, fit. From a study of fragments of the type at the U.S. National Herbarium, it appears that they may be only environmental variants of var. *songarica*. However, since identification is a difficult problem in this genus even with good collections and complete herbarium specimens and since South-east Asia is poorly known, it seems best to defer conclusion concerning these for the present.

This variety was described by Ruprecht from Schrenk's specimens collected by Lake Balkhash (Balchasch). It is represented in this study by the following collections of the senior author. *China*: Triangle City, Kwangtung (A-1347), Hunan Province (A-5638), specific origin unknown (A-5636), Amoy, Fukien (A-726, A-3503, A-2559, A-5635, A-5639); *Formosa*: Koahsuing (A-2582). This variety has escaped cultivation in much of the southern part of the United States and a recent study (Shinners, 1956) reports that it is now found wild in ten counties in Texas.

SUMMARY

From a review of the literature, the geographical distribution of *Bothriochloa ischaemum* is presented as is a brief taxonomic history. Fifty-seven samples of the species from different localities were grown in a uniform nursery at Stillwater, Oklahoma. Herbarium material was made of ten specimens from a random selection of each sample. Both from field notes and a detailed study of the herbarium specimens a morphological analysis was made.

From this analysis two morphological types were established and correlated with geographical distribution and chromosome number.

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The genus Valeriana in East Tropical and South Africa.

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(With 6 Text-figures)

[Read 31 November 1957]

In number of species, the genus *Valeriana* is poorly represented in Africa. At the northern perimeter of the continent, mostly in the Atlas Mountains, two or three valerianas share relatively close morphological affinities with each other and to certain species on the northern side of the Mediterranean. Elsewhere in Africa, the genus contains three well-defined and quite unrelated relict species. The endemic *V. kilimandscharica* and *V. volkensii* of the East African snow mountains are of particular interest in view of their probable relationships with certain Andean species of South America and not to any other known species of the Old World. Interestingly enough, *V. capensis*, the third species considered must be thought of as being most closely related to the *V. officinalis* alliance of the Northern Hemisphere. It can be suggested that the data presented not only document these African species more clearly than has been done heretofore, but also may help to shed more light upon the history and distributional patterns of continental floras.

Relationships of the species

Those discussed are well-marked morphologically. Interspecific relationships between them, such as incipient hybridization do not appear to have complicated the variation patterns of the populations studied. The modern distribution suggests that three outlying vicarious species are involved whose closest relatives are to be found outside the African continent. *V. kilimandscharica* is unique among Old World *Valeriana* in lacking the pappus-like calyx, resembling in this respect some Andean species in South America. The relationships here appear to be closest to *V. alypifolia* and *V. grisiana* of the northern Andes of Colombia and Ecuador. *V. volkensii*, the other Afro-alpine species, whose distribution coincides over part of its range with that of *V. kilimandscharica*, is the only Old World *Valeriana* with a scrambling habit. It most closely resembles *V. decussata* of Peru.

Abbreviations

Following are the herbaria from which specimens were borrowed. Letters in parentheses under citation of specimens refer to the institutions (Lanjouw and Stafleu, in *Index Herb.* pt. 1, ed. 3 (1956)).

BM	British Museum (Natural History), London.
EA	The East African Herbarium, Nairobi.
G	Conservatoire et Jardin Botaniques, Genève.
K	Royal Botanic Gardens, Kew.
MO	Missouri Botanical Garden, St Louis.
P	Muséum National d'Histoire Naturelle, Paris.
PRE	National Herbarium, Pretoria.
SAM	South African Museum, Cape Town.
SBT	Naturhistoriska Riksmuseum, Stockholm.
UPS	University of Uppsala, Uppsala.

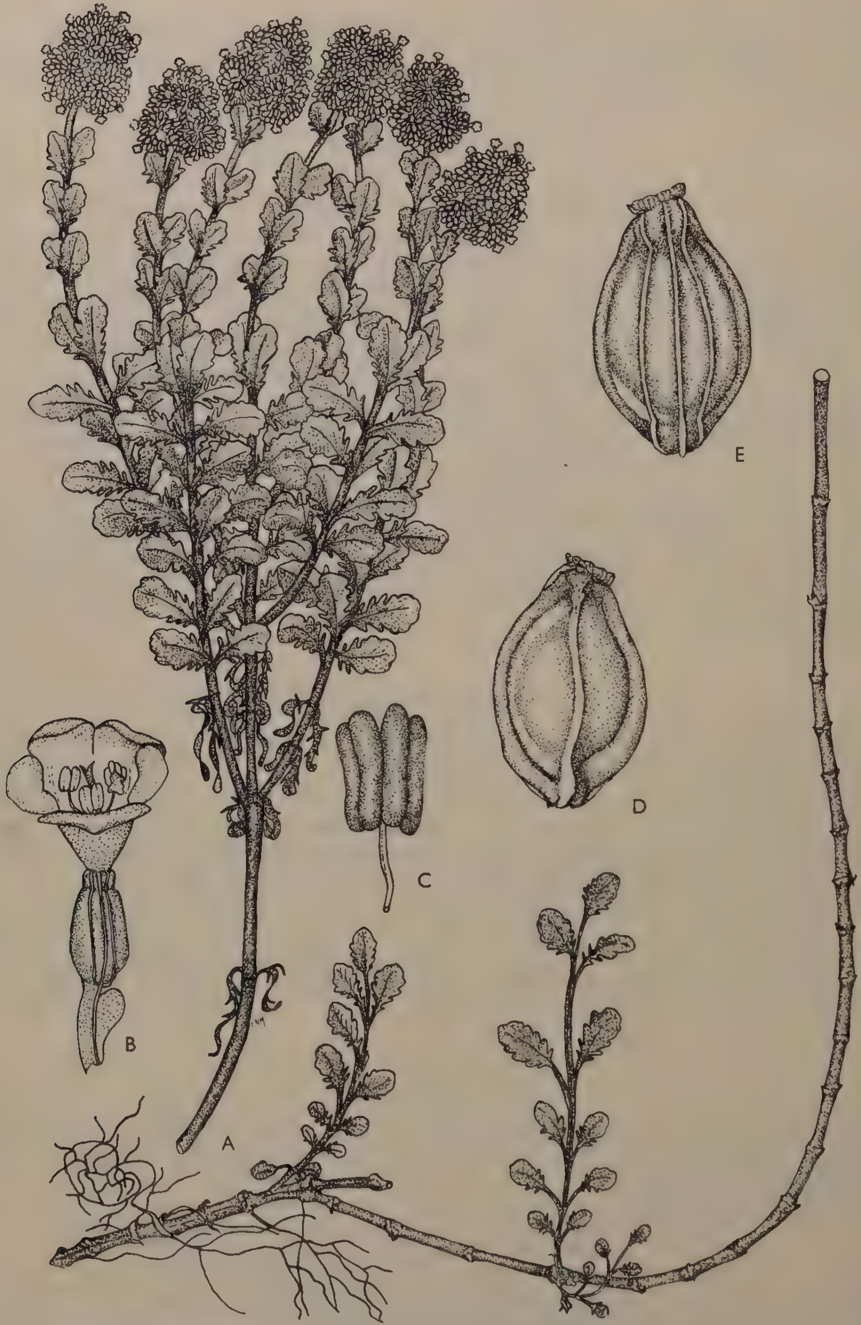


Fig. 1. *V. kilimandscharica* Engl. A, whole plant, natural size, Hedberg 961; B, flower with attached achene, × 25, Hedberg 961; C, stamen prior to anthesis, × 50, Hedberg 961; D, achene, adaxial view, note cupuliform calyx, × 25, Taylor 3503; E, achene abaxial view, × 25, Taylor 3503.

KEY TO THE SPECIES

A. Leaves predominantly shallowly rounded-dentate, rarely almost entire; calyx-limb undivided, short cupuliform, more or less dentate; Mts. Aberdare, Kenya, Elgon, Kilimandjaro. 1. *V. kilimandscharica*

AA. Leaves predominantly pinnately divided, or if undivided then entire or irregularly serrate; calyx-limb pappus-like.

- B. Stems branched at the nodes; plants clambering; achenes elliptic to oval-patelliform, 2·5–4·0 mm. long; Mts. Elgon and Kilimandjaro. 2. *V. volkensii*
- BB. Stems unbranched at the nodes; plants not clambering; achenes broadly ovate to ovate-oblong, 2·5–5·5 mm. long; Mt. Kenya south to the Cape Peninsula. 3. *V. capensis*

ENUMERATION OF THE SPECIES

1. **Valeriana kilimandscharica** Engl.

Valeriana kilimandscharica Engl., in Engl., *Bot. Jb.* **19**, Beibl. no. 47, 48 (1894). Holotype: *Volkens* 1533 (G, K, PRE).

V. elgonensis Mildbr., in *Not. Bot. Gard. Mus. Berl.* **8**, 234 (1922), t. 6 (1923). Holotype: *Granvik s.n.* (SBT).

V. aberdarica T.C.E. Fr. jr., in *Not. Bot. Gard. Mus. Berl.* **8**, 413, t. 6 (1923). Holotype: *Fries* 2471 (SBT, UPS).

V. keniensis T.C.E. Fr. jr., in *Not. Bot. Gard. Mus. Berl.* **8**, 412, t. 6 (1923). Holotype: *Fries* 1379 (SBT, UPS).

Perennial (1–) 2–9 dm. tall (apparently evergreen), more or less tufted, suffrutescent, rhizomatous subshrub, scrambling to reclinate or erect, slender to relatively coarse, rooting at the nodes from the creeping horizontal stems; *rhizomes* 1–2 mm. thick, slender, the internodes 1–3 cm. long. *Stems* at least below somewhat woody, naked, more or less tufted, rather profusely branched near ground-level, mostly leafy above, the internodes predominantly 3–10 mm. or sometimes up to 3 cm. long, quadrangular in × -section towards the summit, mostly terete below, the pith continuous, tawny to brownish. *Leaves* membranous, mostly cauline, spatulate, (0·9–) 2·0–4·1 cm. long, (0·3–) 0·6–1·5 cm. wide on the flowering shoots, (2·5–) 3·2–4·7 cm. long, (0·7–) 0·9–1·4 cm. wide on the vegetative shoots, obtuse to acute, shallowly rounded-dentate, sometimes more or less pinnatifid on the rachis (petiole) below, the lobes diminutive or entire, the lower old leaves becoming brownish marcescent, uniformly pilosulous or glabrous. *Inflorescence* an aggregate dichasium, frequently globose to somewhat elongate (0·8–) 1·5–4·5 cm. long, (0·8–) 1·3–1·8 cm. wide in anthesis, at maturity, becoming somewhat more elongate and spreading, 1·0–4·5 (–8) cm. long, 0·9–2·5 cm. wide, the internodes pilosulous, the ultimate dichotomies rather densely aggregated, the subtending floral bracts cuneate-truncate, chartaceous, hyaline or pinkish, 2·0–4·0 mm. long, longer than the achenes; flowers nearly always perfect (plants occasionally gynodioecious). *Corolla* rotate, 5-lobed, 1·5–2·5 mm. long, barely gibbous, the lobes essentially equal or just barely irregular, about as long as the tube, white, pink to purple or brownish red, glabrous throughout. *Stamens* 3, included, the anthers 4-lobed. *Style* 3-lobed, included in perfect flowers, slightly exserted in pistillate flowers. *Achenes* broadly ovate to ovate-oblong, 1·7–2·6 mm. long, 1·0–1·7 mm. wide, glabrous or pubescent, brown. *Calyx-limb* short cupuliform, more or less dentate. ($2n=16$ *fide* Hedberg, Uppsala.)

Type locality

'Kilimandscharo: in einer feuchten Schlucht oberhalb des Kibosch-Waldes, Yumba ya Mbassa, um 3100 m, häufig—blühend und fruchtend im Januar 1894.'

Distribution

Alpine meadows, tussock grassland and heath bogs, also along small streams and on wet rocks, 9500–15,000 ft. alt. Flowering and fruiting throughout the year.

MT. ABERDARE. Kinangop moorlands, 11,000 ft. alt., *Dale 2694* (EA, K); Satiema, 3800 m. alt., *Fries 2471* (SBT, UPS); Kinangop, *Fries 2471a* (SBT, UPS); Kinangop, northern slopes in Ericaceous belt, 3400 m., *Hedberg 1549* (UPS).

MT. KENYA. 10,000 ft. alt., *Armstrong 3665* (EA, K); 12,000 ft. alt., *Burrows 10035* (EA), *Fries 1379* (SBT, UPS); in valle Teleki, *Fries 1379b* (UPS); Hobley Valley, 14,000 ft. alt., *Greenway 1941* (EA); in tussock grassland, Teleki Valley, 4200 m. alt., *Hedberg 1699* (UPS); among wet rocks, 15,000 ft. alt., *Meinertzhagen 9392* (BM, EA); ridge between Sanec and Serimon, 13,800 ft. alt., *Rogers 601* (K).

MT. ELGON. Crater, 13,000 ft. alt., *Adamson 476* (K); 13,000 ft. alt., *Bally 4031* (K); 13,000–14,000 ft. alt., *Battiscombe K676* (EA); 13,600 ft. alt., *Dale 3180* (EA); Sasa Camp, heath bog, 10,500 ft. alt., *Forbes 261* (K); without definite locality (T: *V. elgonensis*), *Granvik s.n.* (SBT); 4000 m. alt., *Granvik 105* (SBT); in the crater, 4050 m. alt., *Hedberg 961* (UPS); eastern slopes above Tweedie's saw-mill, 3450 m. alt., *Hedberg 210* (UPS); Koitobbon, 4000 m. alt., *Holm 2* (SBT); 13,000 ft. alt., *Lindblom s.n.* (SBT); 13,500 ft. alt., *Lugard 404* (EA, K); Bulambuli stream, 9500 ft. alt., *Synge 876* (BM, MO); Jackson's summit, among rocks, *Synge 1906* (BM); Masaba, alpine meadow, 13,650 ft. alt., *Thomas 617* (EA, K); near Bulambuli, 10,500 ft. alt., *Tothill 2441* (K).

MT. KILIMANJARO. Below Peter's Hut, 11,000 ft. alt., *Cotton 50* (K); near Peter's Hut, 12,000 ft. alt., *Greenway 3749* (EA, K); Shira Mts., 13,000 ft. alt., *Haarer 1140* (EA, K); above Marangu in the Philippia region, 3800 m. alt., *Hedberg 1227* (UPS); above Machame, 10,000 ft. alt., *Moreau 86* (EA, K); above Machame, 13,000 ft. alt., *Moreau 87* (EA); Gürtelwald, 3000 m. alt., *Schlieben 4469* (BM, SBT); with Ericaceae, *Alchemilla*, and *Euryops*, 12,000 ft. alt., *Verdcourt and Eastop 1218* (MO).

V. kilimandscharica occurs as part of the Afro-alpine flora of Mts. Aberdare, Elgon, Kenya, and Kilimanjaro. Nearly 35 years ago, the Swedish botanists, Robert and Thore Fries described *V. aberdarica* from Mt. Aberdare and *V. keniensis* from Mt. Kenya. A third collection by Granvik made about the same time from Mt. Elgon, purportedly a third species, *V. elgonensis*, was described by Mildbraed in Berlin. The brothers Fries came to the conclusion that East African mountain peaks supported closely related but distinct vicarious species in some plant genera. This point of view, although prevalent during the early days when a paucity of specimens characterized the tenor of most taxonomic work, cannot any longer be supported on face value in view of the quantities of recently collected materials from the East African mountains.

It is true that geographical discontinuity does characterize the distribution pattern of *V. kilimandscharica*. However, infraspecific differentiation into varieties or subspecies would not appear to follow automatically as a result of such discontinuity. The mode of variation over the total distribution of this species strongly suggests, in spite of distributional discontinuities, that continuous variation is operating and that the populations are, as a matter of fact, relatively well stabilized. Further collecting would no doubt justify this conclusion. Single character differences are manifest most conspicuously by the achenes, whether glabrous or pubescent. However, this is of relatively little importance when considering the unreliability of indument of the achenes as a good specific character in *Valeriana*.

The absence of the pappus-like calyx is paralleled in the Andean species of South America with cupuliform calyces.

2. **Valeriana volkensii** Engl.

Valeriana volkensii Engl., in Engl., *Pflanzenw. Ost-Afr.* pt. C. 395 (1895). Holotype: *Volkens 1917* (K), isotype (G).

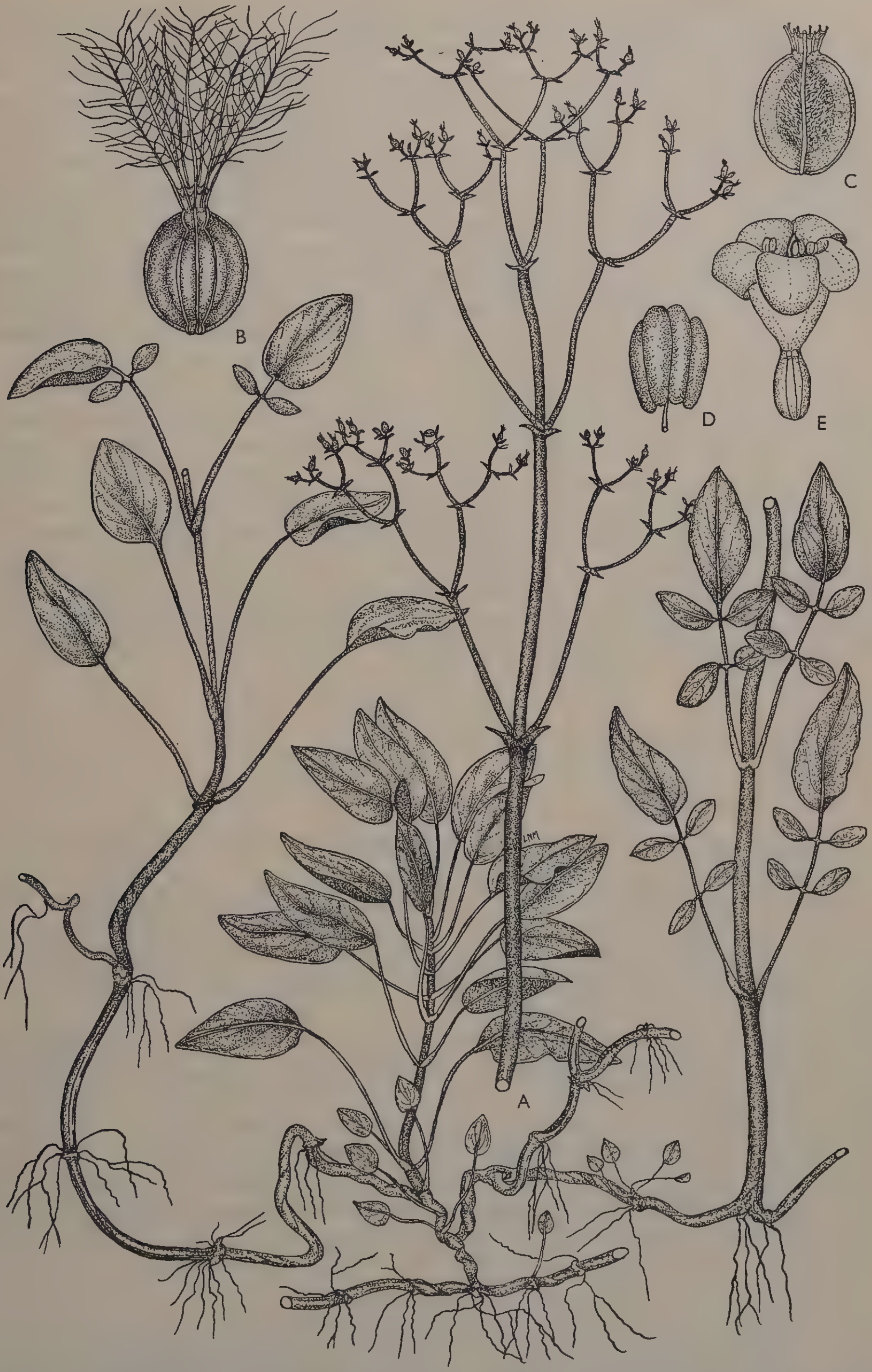


Fig. 2. *V. volkensii* Engl. A, whole plant, natural size, Schlieben 4823; B, achene, abaxial view, × 10, Synge 1872; C, achene, adaxial view, × 10, Synge 1872; D, stamen prior to anthesis, × 20, Synge 1092; E, flower with attached achene, × 10, Alluaud 155.

Perennial (apparently partially evergreen) herb, 6·8–10·0 (–18) dm. tall, simple or branched, slender, rhizomatous, sometimes stoloniferous, rooting at the nodes. *Stems* mostly clambering or erect, 1·5–5·0 mm. thick, mostly naked below, branched on the nodes above, the new shoots leafy, the internodes 0·5–1·0 cm. long on the growing shoots, fistulose, the nodes solid, terete to more or less quadrangular, uniformly scattered to relatively dense, appressed or straight pilosulous. *Leaves* membranous, mostly cauline, impari-pinnate, rhombic in broad outline, largest at the base, grading smaller and becoming bract-like towards the inflorescence or undivided and ovate, glabrous or sparingly pilosulous on both sides, mostly on the nerves, crenulate, the diminutive sinuses glandular, the rachis (dilated at the base) and terminal leaflet of the divided leaves 4·4–16·5 cm. long, the terminal leaflet 1·8–6·5 cm. long, 0·6–3·4 cm. wide, acute to short acuminate, the lateral leaflets 1–4 pairs, somewhat oblique, short petiolate, grading smaller, the undivided leaves 3–4 cm. long, ovate, the petiole 4·5–4·8 cm. long, dilated at the base, the older leaves drying below and becoming brownish marcescent. *Inflorescence* an aggregate dichasium, 12–24 cm. long, 4–5 cm. wide in anthesis, in fruit widely diffuse, 18–50 cm. long, 8–20 cm. wide, the internodes glabrous or scattered pilosulous, the nodes tufted pilosulous, linear-bracteate, becoming oblong-bracteate towards the ultimate dichotomies; flowers perfect (in those seen). *Corolla* infundibuliform, gibbous, somewhat irregular, 1·5–3·0 mm. long, the lobes one-third to one-half the length of the tube, white to pale pink, the throat glabrous within. *Stamens* 3, included, the anthers 4-lobed. *Style* barely 3-lobed, almost capitate. *Achenes* elliptic to oval-patelliform, 2·5–4·0 mm. long, 1·5–3·0 mm. wide, smooth, spreading pilosulous on the adaxial side, glabrous on the abaxial or glabrous on both sides, the adaxial margins more or less winged or plane. *Calyx-limb* 8–13-fid.

Type locality

'Kilimandjaro, Useriwald, 2700 m. Marz 1894.'

Distribution

Forest glades near water, moist rocky stream banks in bamboo zone, 8100–11,200 ft. alt. Flowering and fruiting January–August.

MT. ELGON. Uganda, bamboo zone, 9000–10,000 ft. alt., *Dümmer 3577* (K); eastern slope above Tweedie's saw-mill, 3450 m., *Hedberg 257* (UPSV); 10,500 ft. alt., *Lindblom s.n.* (SBT); Uganda, Bulambuli, Bugishu district, 9500 ft. alt., *Synge 1872* (BM); 11,200 ft. alt., *Taylor 3564* (BM, MO); 9000 ft. alt., *Tothill 2357* (K); forest glade near water, 8800 ft. alt., *Tweedie 892* (K).

MT. KILIMANJARO. Zone des prairies, 3200 m. alt., *Alluaud 155* (P); Kimenzaliz stream, above Rongai, 8800 ft. alt., *Rogers 438* (BM, EA, K); Bergwiesen, 2800 m. alt., *Schlieben 4823* (BM, SBT).

V. volkensii occurs as a part of the Afro-alpine flora of Mts. Elgon and Kilimanjaro above 8100 ft. altitude. This species differs from all other Old World *Valeriana* in the branched aerial stems, the clambering growth habit, and the elliptic to oval-patelliform achenes. The obvious relationships of *V. volkensii* lie with some of the scandent Andean species of South America, notably *V. decussata* of Peru.

3. **Valeriana capensis** Thunb.

Valeriana capensis Thunb. *Prod.* **7**, 1794. Holotype: *Thunberg s.n.* (photo MO, UPSV).
V. capensis Thunb. var. *lanceolata* N.E.Br. in *Kew Bull.* **146** (1895). Holotype: *Evans* 368 (K, photo MO).

Perennial, gynodioecious herb, (1·2–) 4–8 (–14.0) dm. tall in flower, 1·5–10·0 dm. tall in fruit (high altitude plants sometimes depauperate), slender, sometimes delicate but mostly relatively coarse and robust; rhizomes ramifying more or less parallel with the ground-level, 3–7 mm. thick, the fibrous roots relatively thickened fusiform, 2–4 mm. in diameter, 3–15 cm. long, usually rather densely fasiculate on the rhizome at ground level or 1–2 in. below, the plants sometimes stoloniferous. *Stems* erect, herbaceous, usually tufted leafy at the base near ground-level, with about 3–5 pairs of cauline leaves, about (1–) 3–4 (–9) mm. thick, tawny, the nodes solid, uniformly dense hairy, rarely smooth (in dried material), usually with shallow parallel ribs the full length, terete or somewhat angled, glabrescent to relatively densely short, soft hairy. *Leaves* membranous, the cauline, 3–5 pairs, those at the base frequently loosely tufted, lanceolate or rhombic to oblong in outline, mostly obovate to oblanceolate, predominantly imparipinnate or sometimes pinnatifid, occasionally undivided, the lowermost 7–44 cm. long, (0·9–) 1·7–9·7 cm. wide, the cauline simulating the basal but grading smaller, the uppermost pair bract-like, the terminal leaflet ovate to lanceolate, 2·2–11·4 cm. long, 0·7–5·5 cm. wide, acuminate or acute to obtuse, entire to irregularly dentate, sinuate to repand, green above, more or less glaucous beneath, the lateral leaflets simulating the terminal but grading smaller, with (2–) 4 (–9) regularly or irregularly disposed pairs, essentially sessile, the rachis and leaflets glabrous or uniformly short pilosulous, especially on the veins. *Inflorescence* an aggregate dichasium, 1·5–29·0 (–55) cm. long, 1·3–14·5 cm. wide in anthesis, in fruit 2·5–30·0 (–74) cm. long, 2·5–12·0 (–21) cm. wide, the internodes glabrous or pilosulous along one side, tufted pilosulous at the nodes, the floral bracts 3–4 cm. long, acuminate. *Corolla* infundibuliform, gibbous, somewhat irregular, 1·5–2·5 mm. long in the pistillate flowers, 2·5–5·5 mm. long in the perfect ones, the lobes one-third to one-half the length of the tube, white to pink, lilac or mauve, glabrous without, densely to sparsely white hairy at the base of the throat within. *Stamens* 3, exserted, the anthers 4-lobed. *Style* 3-lobed at the tip, exserted. *Achenes* broadly ovate to ovate-oblong, 2·5–5·5 mm. long, 1·3–2·5 mm. wide, tawny, glabrous. *Calyx-limb* 8–14-fid, the segments spreading.

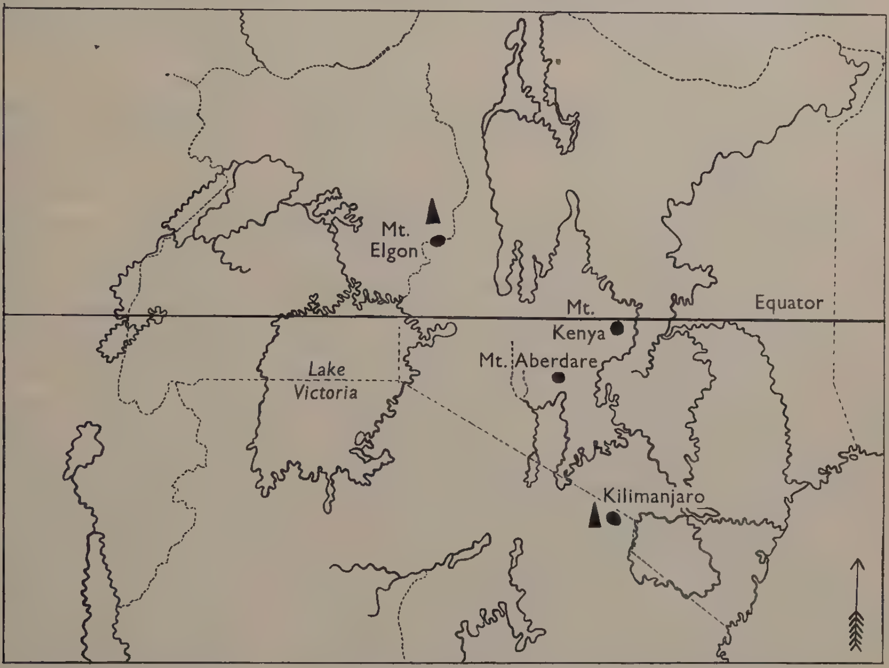


Fig. 3. Distribution of *V. kilimandscharica* Engl. (●) and *V. volkensii* Engl. (▲).

Vernacular name

Tsongarechesa (Southern Rhodesia).

Type locality

'Crescit in Montiam convalliis pone Lange Kloof. Floret Decembri.' (Cf. Hutchinson J., *A Botanist in Southern Africa*, 618 (1946).

Distribution

Stream bank forest, wooded ravines, marshy ground in valleys, pasture edge of wood, mountain grassland, open grassy patches between scrub, peaty soils, sandy soils, reddish orange bauxite soil, under overhanging dripping rock faces, 1800–11,180 ft. altitude. Flowering and fruiting October–May.

Basutoland. Along water courses, Leribe, *Dieterleu 278* (PRE); tributary of Senquayene, 28° 18′ E., 29° 22′ S., *Guillarmod 138* (PRE); Ntibokho Valley, 28° 18′ E., 29° 20′ S., *Guillarmod 264* (PRE); Mamalapi, *Guillarmod 663* (PRE); Mokhotlong, *Guillarmod 1181* (PRE).

Cape Colony. Stutterheim Division, east end of Kabaku Hills, *Acocks 9333* (K, PRE); Baziya Mts., 4000 ft. alt., *Baur 546* (K, paratype of var. *lanceolata*); north side of Kromme River, nr. Wagenboom Stn., Humansdorp, *Burchell 4848* (K, P); Albert District, *Cooper 632* (K, UPS); Paarlberg, *Drège s.n.* (MBG ,P, SAM, SBT); Stormberg, zwischen Klaassmitsrivier und Sternbergspruit, *Drège s.n.* (K, MBG, P, SBT); oberhalb Philipstown, *Ecklon and Zeyher 38.6* (SBT); Winterberg, Kafferland, 5000–6000 ft. alt., *Ecklon and Zeyher 13.12* (SBT); Uitenhaag, am Vanstaadesberg, *Ecklon and Zeyher 4.2* (SBT); Kat River and on Katberg, *Ecklon and Zeyher 6.2* (PRE, UPS); margins of streams, nr. Komgha, *Flanagan 400* (PRE, SAM); Engcoba Mt., *Flanagan 2757* (PRE); Uniondale division, top of Prince Alfred's Pass, 3400 ft. alt., *Fourcade 1298* (SAM); Duine Veld, Slang River, Humansdorp Div., *Fourcade 1848* (K); Featherstone Klog, Grahamstown, *Galpin 339* (PRE); Ben McDhui, Witteberg, Barkly East Div., *Galpin 6653* (K, PRE, SAM), *6654* (K, PRE); mountain side, Queenstown, *Galpin 8308* (PRE); Coldstream, Grahamstown, *Jane 17146* (PRE); Katberg, *Lole 2750* (PRE); Kentani district, *Pegler 197* (BM, K, PRE); Szartkop near Simon's Town, Cape Peninsula, *Pillans 10886* (MBG); Georgetown, *Prior s.n.* (K, PRE); Nord Hoek Mts., Cape Peninsula, *Salter 275/8* (BM); Port St John district, 3600 ft. alt., *Schonland 4126* (PRE); Koudveld, Murraysburg, *Tyson 164* (BM); 3 miles from Amabele, *de Vries 10* (PRE); near Grahamstown, Albany district, *Zeyher 877* (BM, K, SAM); zwischen Katrivier und Witbergen, 5000–6000 ft. alt., *Zeyher 118.11* (SBT); Katrivier, *Zeyher s.n.* (K); Uitenhage *Zeyher s.n.* (BM).

Kenya. Kathita River, Mt. Kenya (north-east sector), *Schelpe 2622* (BM).

Mozambique. Namuli, Makua country, *Lase s.n.* (K).

Natal. Upper slopes, Mt. Aux Sources, *Bayer and McClean 311* (PRE); top of Tabamhlope, 6000–7000 ft. alt., *Evans 368* (K, photo MO); Dooley water, Natal National Park, *Galpin 10389* (PRE); Bergville district, Cathedral Peak Forest Research Station, *Killich 975* (K); Imfulazane, Melmoth, Zululand, *Mogg 6180* (PRE, P); Lidgetton, *Mogg 6741* (PRE); Alexandra district, Dumisa, *Rudatis 777* (BM, K); Giant's Castle, *Symons 100* (PRE); Tweekloof (Altemooi), *Thode A 1163* (PRE); Tabamblofe Research Station, Estcourt region, *West 898* (PRE); Inanda, *Wood 282* (BM); about 20 miles along road between Durban and Pietermaritzburg, Bothas Hill, *Wood 554* (BM); Van Reenen, *Wood 6154* (PRE); Nkandhla, Zululand, *Wood 8851* (P); along railway line, about 8 miles from Greytown, *Wylie 28028* (K, MO, PRE).

Nyasaland. Nyika Plateau, *Benson 1434* (BM); Lichenya Plateau, Mt. Mlanje, *Greenway 6312* (EA, PRE); Mt. Waller, *Sanderson s.n.* (BM).

Orange Free State. Bethlehem district, *Phillips 3157* (PRE); Harrismith district, Platberg, *Puttrell s.n.* (PRE).

Southern Rhodesia. Manika, Inyanga, *Cecil 199* (K); Inyanga, Nyamziwa River, *Chase 355a* (MBG); Nuza ridge, *Gilliland 952* (BM); Stapleford, *Wild 843* (K); Mt. Inyangani, *Wild 1500* (K).

Swaziland. Hlatikulu, *Stewart 2628* (SAM).

Tanganyika Territory. Mbulu district, Hanang and Guruwe, *Burtt 2284* (K); Werther's Peak, Mt. Hanang, Mbulu district, *Greenway 7708* (BM, EA, PRE); Mt. Meru, Arusha district, *Greenway 7807* (EA, K); Mt. Rungwe, Kyimbila district, *Stolz 2258* (BM, K, PRE, UPS).

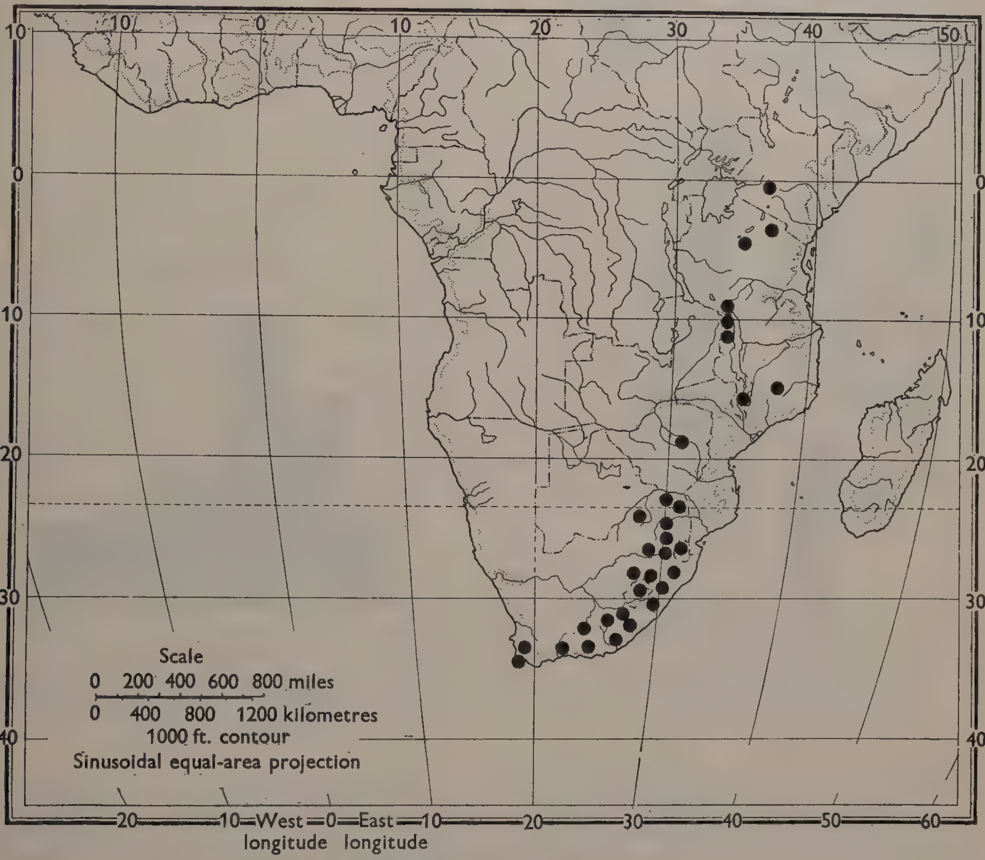


Fig. 4. Distribution of *V. capensis* Thunb.

Transvaal. Kastrol, 7000 ft. alt., *Beeton 168* (SAM); 1 mile north of Haenertsburg, 5000 ft. alt., *Codd 8419* (PRE); Kemps Heights, 12 miles south-east of Lydenburg, 6000 ft. alt., *Codd 8042* (MO); Wakkerstroom, *van Dam 24359* (PRE); Forest station, Woodbush, *van Dam 25636* (PRE); between Pilgrim's Rest and Sabie, *Burtt-Davy 1579* (PRE); in valley, Donkerpoort, Zwaarpruggens district, *Fouché 29* (PRE); Umlomati valley, Barberton, 4000 ft. alt., *Galpin 1133* (PRE); Pilgrim's Rest, *Greenstock s.n.* (BM); Ermelo district, *Henrici 1301* (PRE); Zoutpausberg, 4000 ft. alt., *Hutchinson and Gillett 4194* (K); *Jenkins 10961* (PRE); Heidelberg, *Leendertz 2549* (SAM); Johannesburg, *Leendertz 6158* (PRE); Belfast, *Leendertz 7948* (PRE); Bethal, *Leendertz 9411* (PRE); on river bank, Doringberg Spruit, Lydenburg district, *Liebenberg 3494* (K); Zoutpausberg district, Entabeni, *Obermeyer 31020* (PRE); Spitzkop Ermelo, *Pott 15065* (PRE); Drift Helpmekaar, Woodbush, *Pott 4607* (PRE); Bezuidenhaul's Valley, Johannesburg, *Rand 875* (BM); Carolina, *Rogers 11571* (PRE); Pretoria district, Waterkloof, *Verdoorn 147* (K, PRE); Lydenburg district, bei der stadt Lydenburg, *Wilms 622* (BM, K).

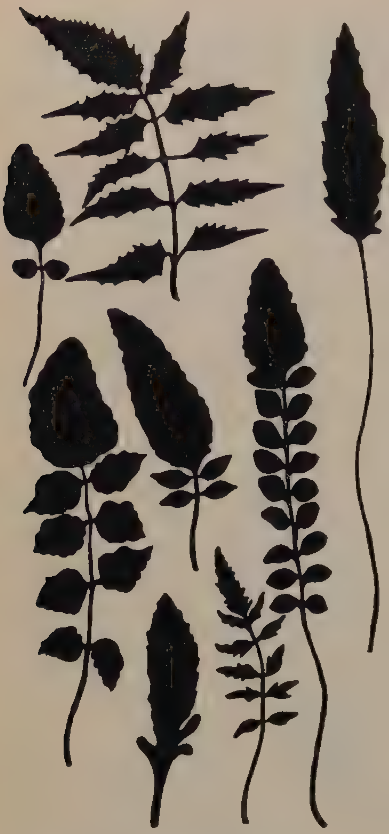


Fig. 5. Variation of the leaves in *V. capensis* Thunb.

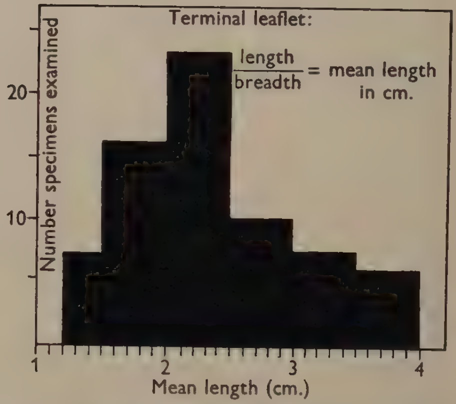


Fig. 6. Histogram showing variation in the mean length of terminal leaflet in *V. capensis* Thunb.

Thunberg, *Fl. Cap.* 33, 1833, first suggested that *V. capensis* was related to *V. officinalis* of Europe. It is clear that these species are related at least historically by way of an ancient intermediate common ancestor. However, the modern populations of *V. officinalis* and *V. capensis* occupy discrete geographical distributions, and gene exchange between the populations could not have taken place within the recent geological past. The African populations manifest morphological discontinuities in leaf shape, fruit size, and flower size which precludes the necessity of merging *V. capensis* with *V. officinalis* into a single polytopic species. By modern reckoning, *V. officinalis* is the basonym of a widely distributed Eurasian *V. officinalis* polyploid complex, and *V. capensis* would be most closely associated with the *V. officinalis-sambucifolia* segment of the complex. Regarding relationship at the subgeneric level, *V. capensis* and *V. officinalis* should be placed in the OFFICINALES series of the genus. The most logical suggestion is that these are vicarious species. They may be considered to be examples of a bipolar distribution of the type discussed by DuRietz (*Acta Phytogeog. Suecica*, **13**, 215–82), whereby certain genera in the northern hemisphere have a counterpart or close relative in the southern hemisphere. This phenomenon is well known for many genera with species pairs in North America and in southern South America. Fewer examples of this kind are known for Europe and southern Africa.

Leaf differences in Valeriana capensis *and* V. officinalis-sambucifolia

capensis	*officinalis-sambucifolia*
1. Terminal leaflet mostly ovate to lanceolate, always larger than the lateral leaflets	1. Terminal leaflet linear to oblong or oblanceolate, rarely ovate; the terminal leaflet two-thirds as long as the lateral leaflets in typical *V. officinalis* but larger in *V. sambucifolia*
2. Leaves mostly pinnately divided, sometimes undivided, mostly obovate or oblong in outline	2. Leaves always pinnately divided, mostly oblong, sometimes obovate in outline

Infraspecific leaf variation in Valeriana capensis

Over seventy-five gatherings of *V. capensis* were examined in the present study. On the basis of leaf variation, the plants may be divided into three rather well-defined categories, irrespective of geographical distribution: (1) leaves lanceolate in outline, the leaflets 8–12 pairs (mostly in the northern part of the distribution); (2) leaves obovate to oblanceolate in outline, the leaflets 3–5 pairs (the most widely distributed variant); (3) leaves undivided or with 1–2 pairs of leaflets (populations of this variant occur both in the northern and southern sectors of the distribution). The variation patterns of the leaves suggest the possibility that infraspecific leaf difference may be associated with discontinuities in distribution and that subspecies or varieties have been thus clearly defined. This suggestion was offered earlier by N. E. Brown who described *V. capensis* var. *lanceolata* with mostly undivided leaves. In the absence of clear-cut geographical discontinuities that would support the differences in leaf shape, subspecific differentiation of *V. capensis* cannot be upheld by the present author.

ACKNOWLEDGEMENTS

The writer wishes to thank Dr Olov Hedberg, of the University of Uppsala, for his kindness in supplying data of value to the present investigation, and the authorities of the institutions mentioned for the loan of specimens which they made available for this investigation. To his wife, the writer is especially grateful for the drawings.

Chromosome numbers in some members of the family Orobanchaceae.

By D. J. HAMBLER

(With Plates **64** and **65** and 7 Text-figures)

[Read 21 November 1957]

PREFACE

This paper represents part of a thesis accepted for the degree of Doctor of Philosophy of the University of London. The work was carried out at Queen Mary College, with the aid of a maintenance allowance from the Department of Scientific and Industrial Research.

PREVIOUS WORK AND SUMMARY

Darlington & Wylie, in *Chromosome Atlas of Flowering Plants* (1955), summarized the chromosome numbers of Orobanchaceae known prior to my letters to *Nature, London*, (Hambler, 1954, 1956). The chromosome numbers of nine *Orobanche* species ($X=(6)$), one *Phacellanthus* species ($X=19$), one *Cistanche* species ($X=20$) and two species of *Lathraea* ($X=?$) are recorded in the Atlas. Only two of the species of *Orobanche* mentioned (*O. ramosa* L. and *O. minor* Sm.) occur in Britain.

During the present author's investigations nine new counts were made for *Orobanche* species, eight of these being from Britain, and one new count for *Cistanche*. The chromosome numbers are listed below and, where possible, herbarium specimens and/or photographs of mature plants from each locality are cited. The material used in this investigation was collected and studied in 1954, except for *Orobanche cernua* var. *desertorum* and *Cistanche tubulosa*, which were received from India and investigated in January 1955, and *Orobanche ramosa*, received from Germany in September 1955.

METHOD

The immature flower spike was used for investigation of mitosis and meiosis. Fixation was in 3:1 (absolute alcohol: glacial acetic acid). Squash preparations of anthers and young ovaries were made with aceto-carmine after soaking in a mordanting solution of iron alum in water. In the case of *Cistanche tubulosa* the material could not be spread adequately until the anthers had been soaked in concentrated nitric acid for 20 min. After this treatment the anther contents appeared as a jelly-like mass (compared with loose pollen mother cells in untreated anthers); squash preparations of this material were satisfactory for chromosome counts.

RESULTS

Genus *Orobanche*—Section *Trionychon* Wallr.

Orobanche ramosa L., $2n=24$ (Pl. **64***a*)

Several preparations of young anthers confirmed the count $2n=24$. This is in agreement with a similar count published by Gardé in 1951, which had not come to the notice of the present author at the time of investigation. The material was collected by Dr P. Eberle from Freiburg im Breisgau, W. Germany, where it was parasitic on tobacco. Specimen in Herb. D. J. Hambler, no. 117.

Orobanche purpurea Jacq., $2n=24$ (Pl. **64***b*, Text-fig. 1)

A count indicating a diploid number of 24 was obtained in a pollen mother cell from each of two plants. Mitotic stages (one being illustrated here) were also counted. The mitotic count being from the sporogenous tissue of a young ovary where the chromosomes were found to be very large. The material originated from a sandy cliff top between Trimmingham and Mundesley, Norfolk, where it was parasitic on *Achillea millefolium* L.; it was collected and determined by the author. A habit photograph and drawings are in Herb. D.J.H. no. 181.

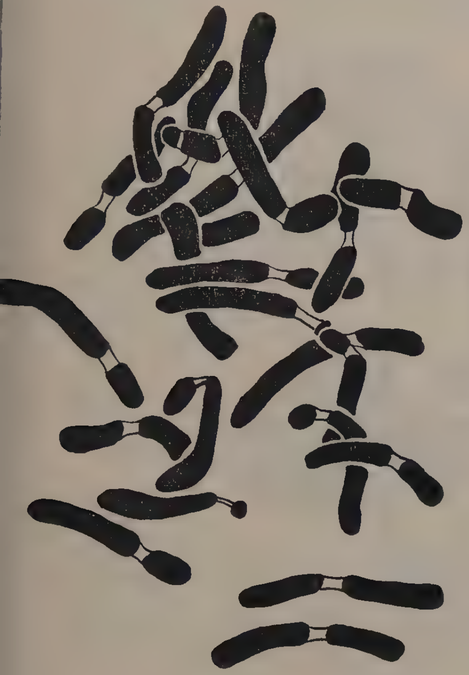


Fig. 1

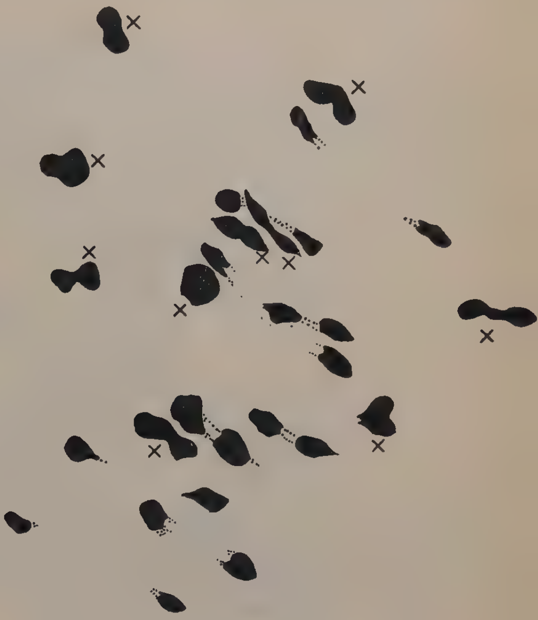


Fig. 2

Text-fig. 1. *Orobanche purpurea* Jacq. mitotic metaphase. × 3000.

Text-fig. 2. *Orobanche rapum-genistae* Thuill. first meiotic anaphase; chromosome pairs not already separated are marked ' × '. Pollen mother cell. × 2000.

Section *Osproleon* Wallr.

Orobanche rapum-genistae Thuill., $2n=38$ (Text-fig. 2)

Meiosis was observed in pollen mother cells from several specimens and the diploid number of 38 is illustrated here by a drawing of first meiotic anaphase (photograph in original thesis). The material originated from a sandy ridge north of road A. 20, west of Hollingbourne, Kent, where it was parasitic on *Sarothamnus scoparius* (L.) Wimmer. It was collected and determined by the author. Specimens in Herb. F. Rose (Maidstone Museum) collected and determined by Dr F. Rose are from the same locality.

Orobanche caryophyllacea Sm., $2n=38$ (Text-fig. 3)

Meiosis in pollen mother cells gave counts of $2n=38$. This number is illustrated here by the drawing. The material originated from sand dunes at Sandwich, Kent; it was collected and determined by the author. Specimens from this locality exist in Herb. F. Rose (Maidstone Museum) collected and determined by Dr F. Rose, and in the herbarium of Queen Mary College (London), in the form of a preserved specimen collected and determined by the author.

Orobanche elatior Sutton, $2n=38$ (Pl. **65**g, Text-fig. 4)

Pollen mother cell meiosis in several spikes indicated a diploid number of 38. This is illustrated by a photograph (Pl. **65**g) interpreted by the drawing. The material originated from chalk downland in a field 1 mile E.S.E. of E. Clandon, Surrey, where it was parasitic on *Centaurea scabiosa* L. It was collected and determined by the author (details of this locality were kindly supplied by J. E. Lousley). A preserved specimen has been placed in the Herbarium of Queen Mary College by the author.

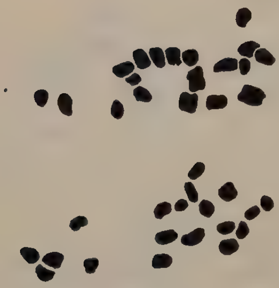


Fig. 3

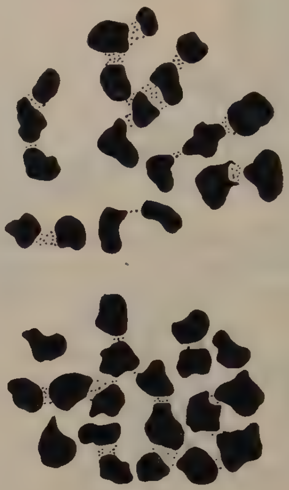
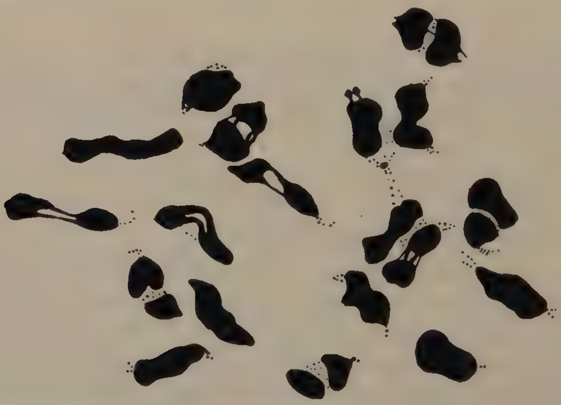


Fig. 4

Text-fig. 3. *Orobanche caryophyllacea* Sm. first meiotic anaphase, 19 chromosomes in each group. Pollen mother cell. × 2000.

Text-fig. 4. *Orobanche elatior* Sutton first meiotic telophase, 19 chromosomes in each group. Pollen mother cell. × 3000.



Text-fig. 5. *Orobanche reticulata* Wallr. first meiotic metaphase; 19 chromosome pairs. Pollen mother cell. × 3000.

Orobanche reticulata Wallr., $2n=38$ (Pl. **64**d, Text-fig. 5)

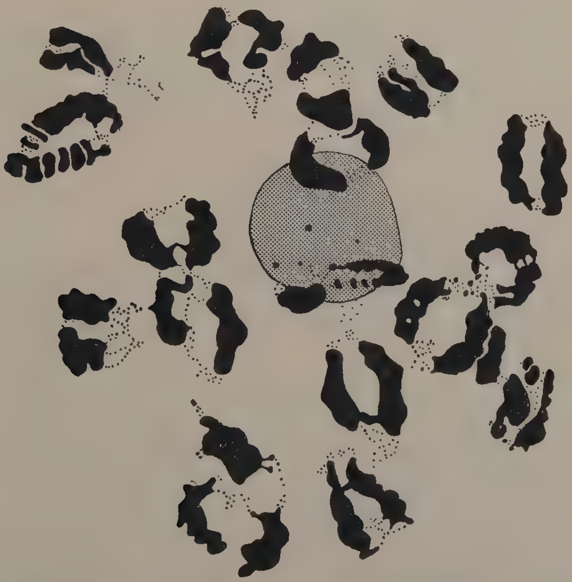
Pollen mother cell meiosis in several spikes confirmed the count of $2n=38$ illustrated by a photograph (Pl. **64**d), and the drawing. The material originated from Ripon, Yorks., where it was parasitic on *Cirsium arvense* (L.) Scop. It was collected and determined by Miss C. Robb. A specimen from this area, collected and determined by E. B. Bangerter (E.B.B. no. 127), is in Herb. Mus. Brit.

Orobanche picridis F. Schultz, $2n=38$ (?)

One spike only of this extremely rare species has so far been investigated and mitotic counts from the tissues of a young ovary indicated the number to be very probably 38. The material originated from the East Cliff, Dover, Kent, and was parasitic on *Picris hieracioides* L. It was determined by Dr F. Rose and collected by the author. Specimens from this locality exist in Herb. F. Rose (Maidstone Museum), collected and determined by Dr Rose, and a photograph in Herb. D. J. Hambler, no. 183 records diagnostic features.

Orobanche hederae Duby, $2n=38$ (Pl. **64***c*, Text-fig. 6)

Pollen mother cell meiosis in three spikes indicated a diploid number of 38. Nineteen bivalents may be clearly seen in the photograph of diakinesis, Pl. **64***c* which is interpreted by the drawing. Material was obtained from the Royal Botanic Gardens, Kew, where it was parasitic on *Hedera helix* L. It was collected (by courtesy of the Director) and determined by the author. A specimen from this locality is in the spirit collection, Kew, collected and determined by R. A. Graham, 3 August 1955.



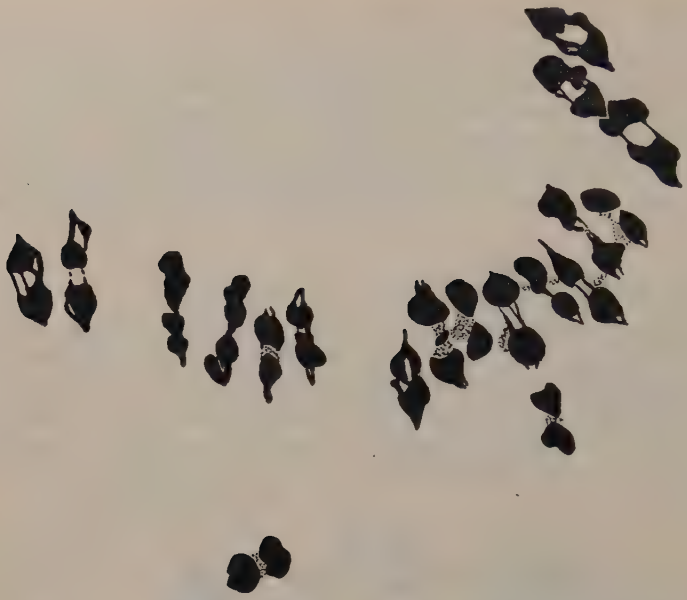
Text-fig. 6. *Orobanche hederae* Duby diakinesis; 19 chromosome pairs. Pollen mother cell. × 3000.

Orobanche maritima Pugsl., $2n=38$ (Text-fig. 7)

Numerous preparations of the anther contents of different specimens confirmed the count $2n=38$, which is illustrated by a drawing (Text-fig. 7). The material was from sand above the high tide mark near Sandwich, Kent, where it was parasitic on *Eryngium maritimum* L. Specimens from the same locality exist in Herb. F. Rose (Maidstone Museum) collected and determined by Dr Rose, and a preserved specimen has been placed in the Herbarium of Queen Mary College by the author.

Orobanche cernua Loefl. var. *desertorum* (Beck Stapf.), $2n=38$ (Pl. **65***f*)

Meiotic stages in pollen mother cells of several spikes indicated a diploid number of 38. A prometaphase of the first meiotic division showing 19 bivalents is illustrated. The material, from Ajmer, India, was collected and determined by Prof. B. Tiagi.



Text-fig. 7. *Orobanche maritima* Pugsl. first meiotic metaphase; 19 chromosome pairs. Pollen mother cell. × 3000.

Genus *Cistanche*

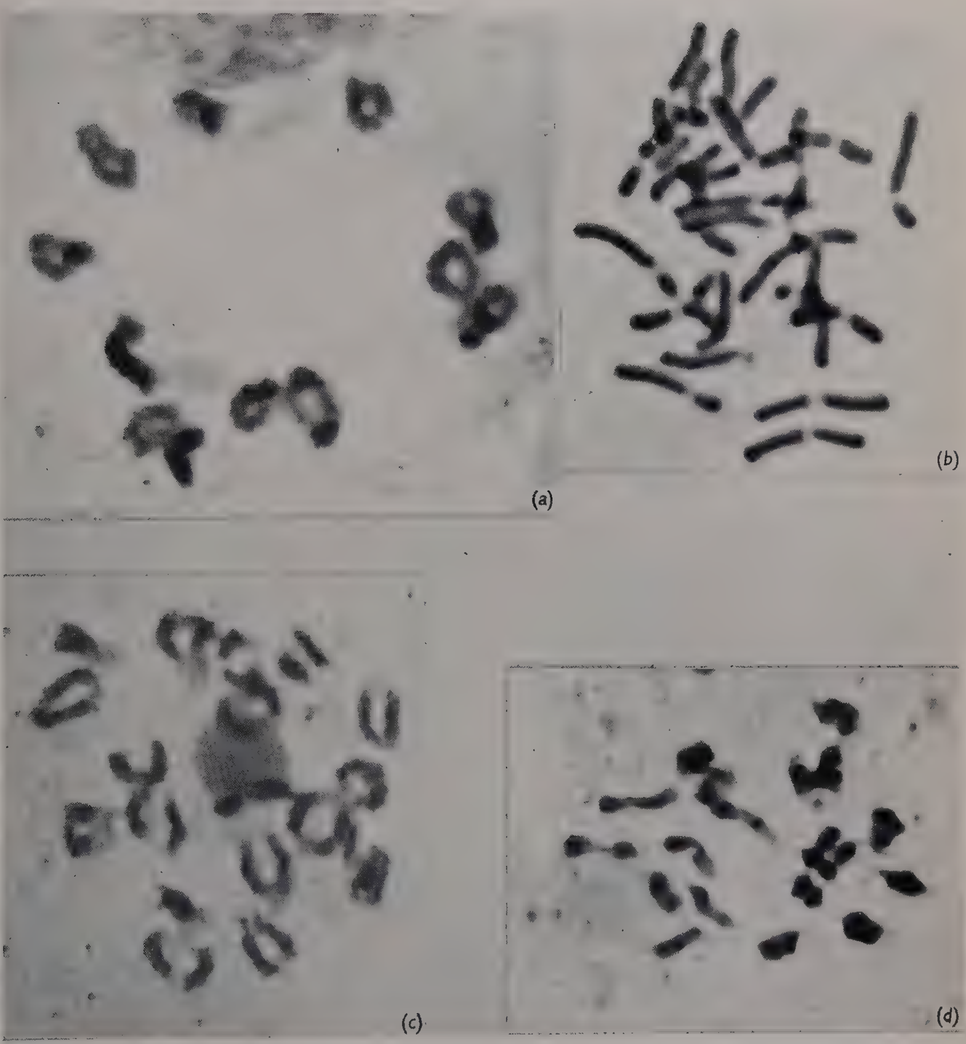
Cistanche tubulosa (Schenk) Hook. F., $2n=40$ (Pl. **65***e*)

After treatment with nitric acid the count $2n=40$ was obtained from several cells in one squash preparation of anther contents. A first meiotic metaphase is illustrated. The material, from Ajmer, India, was collected and determined by Prof. B. Tiagi.

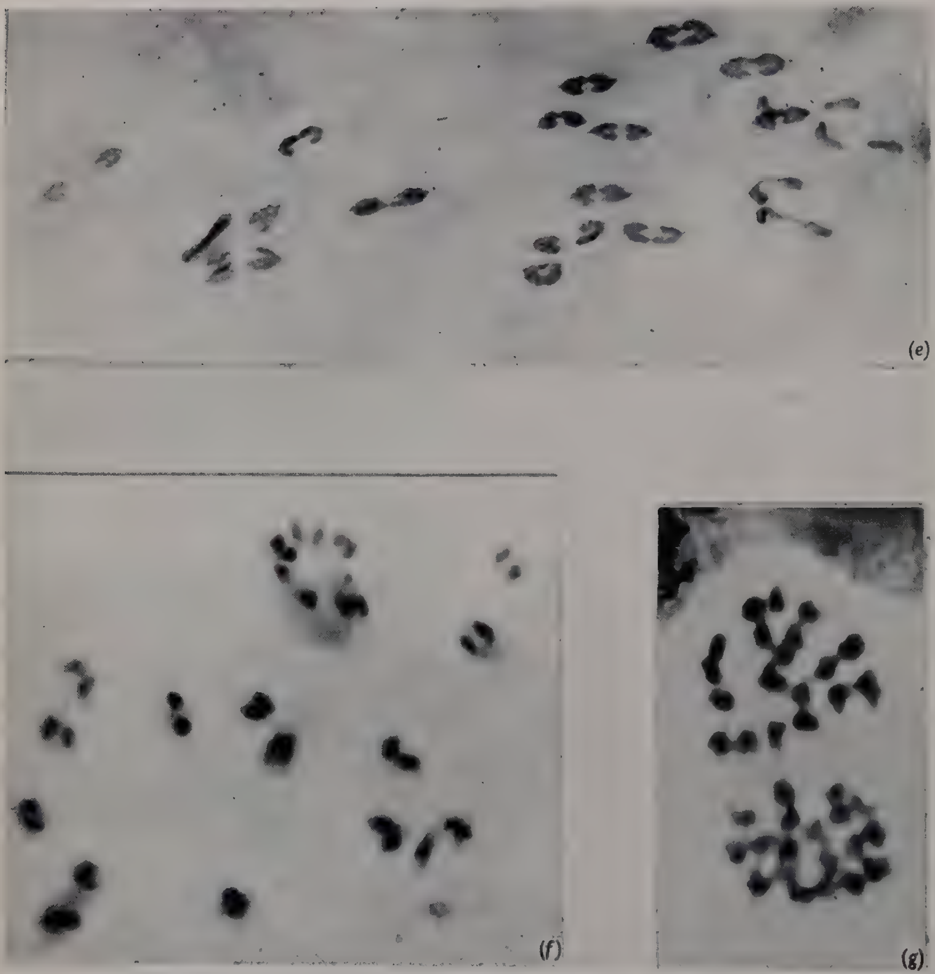
Discussion

Cistanche tubulosa has been shown to possess the same chromosome number $2n=40$ as one other species of the genus (*Cistanche phelypaea* (L.) Cout.) from which a count is recorded in the *Chromosome Atlas of Flowering Plants*. This is the number recorded for a minority of those members of the section *Osproleon* of *Orobanche* so far investigated, and is a number which might easily have been derived (by aneuploidy) from $2n=38$, the number recorded for the majority of the members of *Osproleon*. This may be evidence of intergeneric affinities, although further cytological work is needed before the genealogy of the family Orobanchaceae may be postulated with any degree of confidence.

The species of *Orobanche* for which chromosome counts are recorded here and in the *Chromosome Atlas of Flowering Plants* belong to three of the five sections of the genus recognized by von Mannagetta (1890). The chromosome numbers were at first thought by the author (Hambler, 1956) possibly to reflect the sectional division of the genus, that is: *O. uniflora* L. (section *Aphyllon* Mitchell) with $2n=36$ (and in a parthenogenetic race $2n=72$) ($X=6$) (Jensen, 1951); *O. ramosa* and *O. purpurea* (section *Trionychon* Wallr.) with $2n=24$ ($X=6$); and the seemingly distinct section *Osproleon* apparently characterized by the diploid number 38, or in some cases 40, ($X=19$). The statement by Strivastava (1939) for *Orobanche aegyptiaca* Pers. (*Trionychon*) that 'the haploid number...is 19' is in disagreement with this attractive hypothesis and with part of the hypothetical genealogical tree of *Orobanche* drawn by von Mannagetta from morphological studies. Von Mannagetta's scheme would necessitate independent origin for the number $2n=24$ in *O. ramosa* and in *O. purpurea*. These species are shown on separate



Chromosome complements of Orobanchaceae: photographs from squash preparations.



Chromosome complements of Orobanchaceae: photographs from squash preparations.

branches of the main '*Trionychon*' stock. '*Trionychon*' is represented dichotomizing, one branch bearing *O. ramosa* on one of its ramifications; the other, passing through *O. aegyptiaca*, dichotomizes to give one branch '*Osproleon*' and a smaller branch ending in *O. purpurea*. It may be that *O. aegyptiaca* is a link between the sections *Trionychon* and *Osproleon*, but it is most unlikely, if $2n = 38$ is a typical count, to be ancestral to *O. purpurea*. It might be noted here that *Osproleon* might have arisen from a stock with a basic number of 6 as a result of polyploidy to give $n = 18$, followed by aneuploidy to give the haploid numbers of 19 or 20 characteristic of this section.

When counts become available for other members of the genus, especially for those species with bracteoles, further light will no doubt be shed on this interesting problem.

ACKNOWLEDGEMENTS

I wish first to acknowledge my indebtedness to Dr M. B. E. Godward for her encouragement and interest in my investigations. I wish to thank those botanists who have helped in sending me material, especially Prof. B. Tiagi of Government College, Ajmer, India, for the *Cistanche tubulosa* and *Orobanche cernua* material, Miss C. Rob for *O. reticulata*, and Dr P. Eberle for *O. ramosa*. I wish also to acknowledge those who supplied details of localities, especially the help of Dr F. Rose who kindly supplied me with details of the locations of many *Orobanche* populations. I also acknowledge the payment of travelling expenses for collection of British *Orobanche* by the Department of Scientific and Industrial Research.

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EXPLANATION OF PLATES

PLATE 64

(*a*) *Orobanche ramosa* diakinesis; 12 chromosome pairs. Pollen mother cell. × 2000.
(*b*) See Text-fig. 1 (*O. purpurea*). × 2000.
(*c*) See Text-fig. 6 (*O. hederae*). × 2000.
(*d*) See Text-fig. 5 (*O. reticulata*). × 2000.

PLATE 65

(*e*) *Cistanche tubulosa* first meiotic metaphase (distorted in squashing); 20 chromosome pairs. Pollen mother cell. Material treated with nitric acid. × 2000.
(*f*) *Orobanche cernua* var. *desertorum* first meiotic prometaphase; 19 chromosome pairs. Pollen mother cell. × 2000.
(*g*) See Text-fig. 4 (*O. elatior*). Pollen mother cell. × 2000.

An anatomical approach to the classification of the Musaceae.

By P. B. Tomlinson, Department of Botany, University College of Ghana.

(With 109 Text-figures)

[Read 21 November 1957]

Introduction

Although it is becoming increasingly recognized that the study of the anatomy of the vegetative organs can provide valuable evidence in taxonomic research (for recent examples see Metcalfe, 1951, 1952*a*, *b*; Stant, 1952), the monocotyledons have at present received comparatively little attention from the systematic anatomist. There are a few exceptions, for example the Flagellariaceae (Smithson, 1956), the Xanthorrhoeaceae (Fahn, 1954) and the Zingiberaceae (Tomlinson, 1956).

The Musaceae is a family that presents problems to the botanist because the ways in which the genera of this family have been grouped by successive taxonomists have often shown large differences, as is indicated in a recent and valuable summary by Lane (1955). It is hoped, therefore, that the anatomical observations presented in this paper may be useful in suggesting the most natural grouping of units within the Musaceae. These observations were made for several reasons. First, because it was obvious that the differences of opinion outlined in Lane's paper could only be resolved with the help of additional information of which that provided by anatomy was most wanting. Secondly, I was at the time in Singapore, where material of nearly all genera of the Musaceae was available. Thirdly, because my experience with the anatomy of one other family of the Scitamineae (Zingiberaceae) provided a useful background and starting-point.

Morphology of the Musaceae

Existing ideas, which are so often at variance with each other, about the relationships between the genera of the Musaceae are based almost entirely upon features of vegetative and floral morphology. A survey of these features is presented in Table 1, together with additional notes on the table.

From this summary it is evident that each of the five original genera of which the family was composed is a very distinct entity, and the genera are not likely to be confused one with another. Indeed when one considers the differences between *Orchidantha* and *Ravenala* or *Musa* and *Heliconia* it is not at first apparent that they are related, and this emphasizes the wide range of habit found within the Musaceae.

Classification of the Musaceae

The Musaceae form one of the four families into which the Scitamineae of Bentham and Hooker was subdivided. The other three families, Zingiberaceae, Cannaceae and Marantaceae, all possess combinations of morphological characters which delimit them clearly from each other and from the Musaceae. Consequently, there is no likelihood of confusion between the four groups.

Within the Musaceae itself, no definite agreement has yet been reached as to the way in which its genera are related to each other. Different schemes which have been proposed to subdivide the family are presented in Table 2. From this table it is evident that, with the exception of the last authority, successive writers have emphasized the differences between genera more and more with the result that higher taxonomic units are successively employed. One reason for this is that the workers of the last century

Table 1. *Summary of morphological features exhibited by the genera of the Musaceae*

	Musa[1]	*Ravenala*[2]	*Strelitzia*	*Heliconia*	*Orchidantha*
Life form	Massive herbs with pseudostem from underground corm-like axis[3]	Small trees with woody unbranched erect stem[4]	Small trees with woody stems or rhizomatous herbs	Rhizomatous herbs	Small herbs with erect rhizomes
Leaf arrangement	Spiral	Distichous	Distichous	Distichous or pseudo-distichous[5]	Distichous
Size of leaf sheath	Long (overlapping leaf sheaths produce pseudostem)	Short	Short	Long	Long
Direction of lateral veins of lamina in relation to midrib[6]	± Perpendicular	± Perpendicular	Perpendicular or very oblique	Perpendicular or very oblique	± Parallel
Position of[7] inflorescence and its type of branching[8]	Terminal, racemose	Lateral, racemose	Lateral, racemose	Terminal, racemose	Terminal, cymose
Arrangement of spathes	Spiral	Distichous	Distichous	Distichous or spiral	Spiral
Bracts below individual flowers	Absent	Present	Present	Present	Present
Position of unpaired sepal	Ventral	Ventral	Ventral	Dorsal[9]	Ventral
Distribution of sexes in the individual flowers	Unisexual[10] (monoecious)	Hermaphrodite	Hermaphrodite	Hermaphrodite	Hermaphrodite
Number of stamens	5–6	5–6	5	5	5
Staminode	Absent	Absent	Absent	Present	Absent
Condition of perianth members	Usually five united, one free	Free or united in part	Two dorsal petals form a keel	United in varying degrees	Floral parts united into a solid column. Ventral petal labelloid
Placentation and number of ovules	Parietal or axile, ovules many	Axile, numerous ovules	Axile, numerous ovules	Basal, three ovules only	Axile, numerous ovules
Fruit	Berry, usually indehiscent[11]	Capsule with loculicidal dehiscence	Capsule with loculicidal dehiscence	Berry or capsule with septicidal dehiscence	Capsule
Seed	Non-arillate	Arillate	Arillate	Non-arillate	Arillate
Geographical distribution	Africa, Asia, Oceania	Madagascar, Guiana, Brazil	South-east Africa	American tropics	Malaya, Borneo

Footnotes to Table 1

[1] The genus *Ensete* has recently been separated from *Musa* by Cheesman (1947). While accepting *Ensete* as a distinct genus Lane (1955) points out that it differs from *Musa* in possessing only the following three characters: monocarpic habit, granulose-papillose pollen grains (not smooth), T-shaped embryo (not straight).

[2] The genus *Phenakospermum* has been separated from *Ravenala*, from which it differs in several ways. Thus the inflorescence is terminal or apparently so instead of axillary, there are five stamens instead of six, the ovules are in four rows instead of two, the aril is blue and filamentous instead of red and membranaceous and the embryo is straight and not bent. *Ravenala* in this strict sense contains only one species, *R. madagascariensis*, while *Phenakospermum* includes the two South American species and has been further subdivided into *Phenakospermum* and *Musidendron* by Nakai (1948). Lane (1955) considers that his *Phenakospermum* is more closely related to *Strelitzia* than to *Ravenala*.

[3] Skutch (1927) found in the variety of banana which he studied that the basal buds did not develop in the axils of the leaves but appeared on the side of the stem opposite these, between the two free margins of the leaf sheath. He suggested (Skutch, 1932) that the axis of the banana is really a sympodium, with the apparently lateral buds being terminal buds with their development arrested. As a further extension of this idea the inflorescence could be considered to be lateral.

[4] *Ravenala* (*Phenakospermum*) *guyanensis* is described as having a creeping rhizome and no well-marked aerial stem.

[5] According to Lane (1955) in some species of *Heliconia* the arrangement of the buds on leaf bases indicates that the leaves have a spiral arrangement and that their apparent distichy is due to compression. This condition is called pseudo-distichy and it is suggested that it may be not uncommon in the family.

[6] The juvenile leaves of all genera have a venation which resembles that of *Canna*, with the lateral veins running at an acute angle to the midrib. Consequently juvenile leaves of all members of the Musaceae somewhat resemble the mature leaves of *Orchidantha*.

[7] In those genera with a terminal inflorescence, there is a gradual transition in the shape of the leaves from true foliage leaves to the bracts of the inflorescence. These transitional organs are absent from plants with an axillary inflorescence.

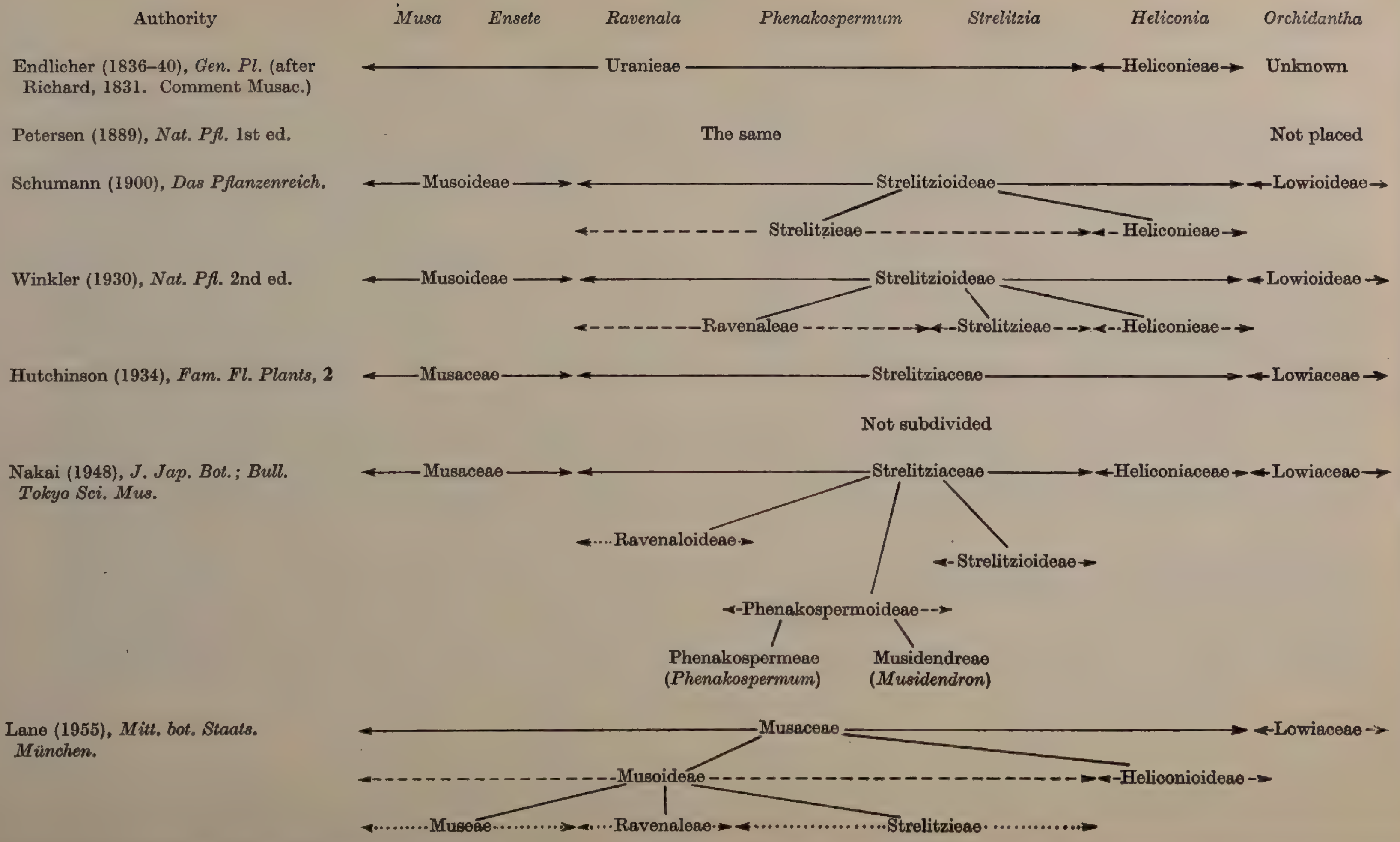
[8] There is still disagreement over the type of branching of the inflorescence in the Musaceae. Fahn (1953), for instance, argues that *Musa* has an inflorescence which is a cincinnus. The interpretations presented in Table 1 are those of Lane which are based on comparative studies between different genera.

[9] The morphology of the flower in *Heliconia*, which is different from that of the other genera in the family, was first clearly established by Eichler (1875). The orientation of the floral parts is inverted as compared with that found in the other genera. Thus in those genera with only five stamens, the absent stamen is a member of the inner staminal whorl and is situated opposite the ventral petal, but in *Heliconia*, this stamen, which is represented by a staminode, lies opposite the dorsal sepal and is a member of the outer staminal whorl.

[10] The unisexual flowers of *Musa* are produced by abortion. Stamens are absent or non-functional in female flowers, the pistil is reduced and non-functional in female flowers.

[11] Although *Musa* is usually considered to have an indehiscent berry, exemplified by the edible banana, a personal communication by Lane indicates that in at least one species, *M. velutina*, the berry splits into three valves to expose the ripe seeds.

Table 2



Authority	*Musa*	*Ensete*	*Ravenala*	*Phenakospermum*	*Strelitzia*	*Heliconia*	*Orchidantha*
Endlicher (1836–40), *Gen. Pl.* (after Richard, 1831. Comment Musac.)	Uranieae					Heliconieae	Unknown
Petersen (1889), *Nat. Pfl.* 1st ed.	The same						Not placed
Schumann (1900), *Das Pflanzenreich.*	Musoideae		Strelitzioideae				Lowioideae
			Strelitzieae			Heliconieae	
Winkler (1930), *Nat. Pfl.* 2nd ed.	Musoideae		Strelitzioideae				Lowioideae
			Ravenaleae		Strelitzieae	Heliconieae	
Hutchinson (1934), *Fam. Fl. Plants,* 2	Musaceae		Strelitziaceae				Lowiaceae
			Not subdivided				
Nakai (1948), *J. Jap. Bot.; Bull. Tokyo Sci. Mus.*	Musaceae		Strelitziaceae			Heliconiaceae	Lowiaceae
			Ravenaloideae	Phenakospermoideae	Strelitzioideae		
				Phenakospermeae (*Phenakospermum*) Musidendreae (*Musidendron*)			
Lane (1955), *Mitt. bot. Staats. München.*	Musaceae						Lowiaceae
	Musoideae					Heliconioideae	
	Museae		Ravenaleae	Strelitzieae			

did not possess as much information as did more recent workers, and the earlier conclusions were therefore more tentative.

However, from Table 2 certain conclusions, for which there is common agreement, become evident. For instance, that *Orchidantha* is somewhat remote from other genera is agreed upon by everyone and, indeed, all later workers are satisfied that it deserves the status of a monotypic family (Lowiaceae). The status of the other genera is less obvious and that which has been awarded to them depends largely on whether similarities or differences between them are emphasized. Thus Nakai divides them into three separate families, but Lane retains them within a single family. Whatever the size of the group involved, on the other hand, all authors agree that *Strelitzia* and *Ravenala* are more closely related to each other than they are to the other genera. No author emphasizes any similarity between *Musa* and *Heliconia*.

MATERIAL AND METHODS

Material

The material used in this investigation was all fixed in formalin–acetic–alcohol. The species concerned, the parts of the plants available, and the sources of the material are given in detail in Appendix B on p. 807.

Methods

In a survey of the present scope it is not possible to describe in detail all parts of even a single species. For this reason sections taken at standard levels in each species were compared as far as possible. The standard levels used were: (i) The lamina and midrib halfway from base to apex of the lamina. (ii) The petiole just below the insertion of the lamina, the upper sheath just below the insertion of the petiole and the base of the sheath at a more arbitrary level. (N.B. The midrib, petiole and sheath are collectively referred to as the 'leaf stalk' in subsequent discussion.) (iii) Central and cortical regions of mature stems. (iv) Mature underground roots.

Three main techniques were used to make microscopical preparations.

(*a*) *Preparations to show the surface layers.* By scraping away unwanted tissue from a piece of the lamina laid flat on a slide, preparations, in which the epidermis and often the hypodermis could be examined in surface view, were readily made. They were cleared in 'Parozone', stained with safranin and Delafield's haematoxylin and mounted in Canada Balsam.

(*b*) *Sections.* Before the material could be sectioned satisfactorily it was sometimes necessary to desilicify it by soaking overnight in hydrofluoric acid. Material treated in this way must be washed for several hours in running water before it can be placed on the microtome.

Two methods were used in section cutting. Unembedded material was sectioned on a 'Reichert' sledge microtome. Other material was embedded by boiling for a few minutes in a 2 % agar solution, in which it was then allowed to solidify in small Petri dishes, and sectioned on a freezing microtome. This second technique was applied to the leaf stalk which contains large air canals, and which collapses when clamped on a microtome in the ordinary way.

Sections were cut from 15–100μ thick. Most observations were made on unstained sections mounted in glycerine. A number of sections were made permanent by double staining with safranin and either Fast Green or Delafield's haematoxylin and mounting in Canada Balsam.

Delicate sections of the large leaf stalks of the Musaceae, cut on the freezing microtome, have to be handled by a special technique. The method adopted, devised by Moore (1954), involves floating the section, in water, on to a slide smeared with egg albumen adhesive and then allowing the section to dry out completely. The slide is then warmed and plunged immediately into 95 % alcohol. The section becomes affixed to the slide, usually without collapse of its cells, and can then be handled in the same way as wax-embedded sections which have been cemented to slides.

(*c*) *Maceration*. This was used to isolate tracheal elements for their study. Small slivers of material were macerated in 20 % chromic acid for about 15 min., after a preliminary boiling for a few minutes in a 10 % caustic potash solution.

ANATOMY OF THE MUSACEAE AS A WHOLE

The most comprehensive account of the anatomy of the Musaceae is that by Solereder & Meyer (1930). In it, all available information is summarized and many new observations are recorded for the first time. Information from that account which is quoted in this paper does not cite the original author, but always 'S. & M.'. More recently the anatomy of the 'Gros Michel' banana has been studied in great detail by Skutch (1927, 1930, 1932), but no comparable study has been made of any other member of the family.

Lamina

Leaf dorsiventral. **Hairs** absent, except for uniseriate hairs on the leaf sheath of *Heliconia illustris* (S. & M.). **Epidermis** wholly or partly cutinized, often with a distinct cuticle on the abaxial surface. Adaxial epidermis uniform, costal and intercostal regions not distinguishable; cells arranged in distinct files parallel to the main lateral veins, the longitudinal direction of the files being ± parallel to the midrib in *Orchidantha*, and ± perpendicular to the midrib in *Heliconia*, *Musa*, *Ravenala* and *Strelitzia*. Adaxial files above the anticlinal walls of the hypodermal cells sometimes composed of slightly larger cells than those elsewhere; the cells usually being rectangular, elongated in surface view, or sometimes square or transversely extended. Abaxial epidermis differentiated into costal and intercostal bands in all genera except *Orchidantha*; cells in the costal regions similar to those of the adaxial surface, but intercostal cells not obviously in files, or with the files displaced laterally beside the stomata, the cells always being very irregular in shape. Walls of the abaxial epidermal cells never conspicuously thickened, but outer tangential walls always distinctly thicker than the others; anticlinal walls linear in surface view except in *Heliconia*, with markedly undulate walls. **Stomata** often present on the adaxial, but always less numerous than on the abaxial, surface; those on the abaxial surface limited to the intercostal regions. Stomata in *Ravenala*, *Strelitzia* and many species of *Heliconia* also absent below the transverse commissures and restricted to short rectangular areas of the intercostal regions. Stomata never in regular files; guard cells each enveloped by a thin-walled lateral subsidiary cell with its long axis parallel to the stomatal pore and usually more anticlinally extended than the other epidermal cells. Cells adjacent to the poles of the stomata, except in *Orchidantha*, shorter than the others and usually recognizable as terminal subsidiary cells. Other epidermal cells adjacent to the stomatal apparatus sometimes modified but not in any regular manner. Guard cells sunken in stomatal depressions, often occluded by cuticular material, in *Ravenala* and *Strelitzia*; always with two cutinized ledges, the wall beneath these somewhat thickened in the median part of each guard cell, especially in *Orchidantha*. Stomatal pores always parallel to the main lateral veins. **Hypodermis** present beneath both surfaces in all genera, and consisting of thin-walled, colourless, enlarged cells, cubical or elongated, or transversely extended and appearing hexagonal in surface view. One colourless hypodermal layer beneath each surface in *Heliconia*, *Orchidantha*, and some *Musa* spp.; more than one layer beneath the adaxial epidermis in *Ravenala*, *Strelitzia* and other *Musa* spp. Abaxial always less conspicuous than the larger-celled adaxial hypodermis. Hypodermal cells adjacent to the circular substomatal chambers either arranged concentrically (*Ravenala*, *Strelitzia*), or in an angular manner (*Heliconia*, *Musa*, *Orchidantha*); those in the costal regions often smaller than those elsewhere, or enlarged as 'expansion cells' (q.v.). **Mesophyll**; adaxial palisade tissue well developed in all genera, except *Orchidantha* with its mesophyll of irregularly distributed large and small cells; spongy tissue consisting of compact, and rounded, or looser, lobed cells in *Heliconia*, *Ravenala* and *Strelitzia*; in *Musa* replaced by longitudinal septate **air-canals** alternating with the veins, and lined with assimilating tissue, its transverse septa being wholly parenchymatous or sometimes containing transverse **vascular commissures**. Somewhat similar transverse commissures and septa noted in *Ravenala* and *Strelitzia*. Fibres or fibre bundles, independent of the vascular system, present in association with the hypodermal layers only in *Orchidantha*. Apparent independent fibre bundles, consisting of longitudinal extensions of sheaths of the vascular bundles occasionally noted in other genera.

Longitudinal veins few and remote from each other in *Orchidantha*, more numerous in *Heliconia*, and very close together in *Musa*, *Ravenala* and *Strelitzia*. Vascular bundles situated closer to the adaxial surface in *Orchidantha* than in the other genera. Vascular bundles often connected to one or both leaf surfaces by vertical buttress-like extensions of the bundle-sheaths; only adaxial buttresses noted in *Orchidantha*; adaxial buttresses restricted to the main vascular bundles in *Heliconia*; all bundles buttressed to both surfaces in *Musa*, *Ravenala* and *Strelitzia*. Bundle-sheaths usually fibrous above and below the vascular tissue in each bundle, but with their lateral parts always parenchymatous and often more than 1-layered in all genera except *Orchidantha*. **Transverse veins** in *Orchidantha* abaxial and with large fibrous sheaths; those in the other genera situated at a median depth in the lamina and sheathed by thin-walled, or, in *Ravenala* and *Strelitzia*, by slightly thick-walled, parenchyma; embedded in vertical parenchymatous septa in *Musa*, *Ravenala* and *Strelitzia*.

Unrolling of the lamina controlled by variously situated, enlarged cells of the hypodermis, termed **expansion cells**. Expansion cells of *Musa* forming a longitudinal 'pulvinar band' (Skutch, 1930), at the junction between the lamina and the midrib and there causing a diurnal movement of the lamina. Other expansion cells of all genera, except *Orchidantha*, arranged in bands on the adaxial side of the main lateral veins.

Midrib, petiole, leaf sheath

Longitudinal **air-canals** extend from the distal parts of the leaf insertions in all genera, the canals being arranged in one or more distinct arcs as seen in transverse section, the number and arrangement of the arcs being characteristic for each genus. Air-canals bounded laterally by thin, parenchymatous, vascularized partitions, and segmented at regular intervals by **transverse diaphragms** of 1–4 layers of loose parenchymatous cells, some of the layers being made up of stellate cells. **Vascular bundles**, as seen in transverse section, somewhat similarly arranged in all genera, but with obvious intergeneric differences. Main veins of the lamina represented in transverse sections of the leaf stalk, taken at any level, by an arc of large vascular bundles (referred to as its main arc), several more abaxial arcs of smaller, shorter bundles also being present, together with bundles of fibres in the ground tissue close to the abaxial surface of the petiole. Structure of the individual bundles as described by S. & M., and similar to that recorded by Tomlinson (1956) for other members of the Scitamineae. Characters of the leaf stalk, additional to those just cited, and possessing generic diagnostic value, include the following: (i) small vascular and fibre bundles close to the adaxial surface in *Heliconia*, *Musa* and *Orchidantha*; (ii) a clearly defined chlorenchymatous band, abaxial in *Ravenala* and *Strelitzia* and adaxial in *Heliconia* and *Musa*; (iii) diffusely distributed chlorenchyma in *Orchidantha*; (iv) peripheral layers of partially sclerosed ground parenchyma in all genera except *Orchidantha*, the more detailed distribution of this tissue being of value for the identification of genera or even species.

Stem

Fundamentally similar in all genera despite their considerable morphological diversity; common characteristics including (*a*) a distinct **cortex** containing a system of discrete, collateral vascular bundles each with a well-developed fibrous sheath adjacent to the phloem only; (*b*) occasional secondary **periderm** arising by division of cells in the outer cortical layers; (*c*) frequent **fibre bundles** present in the outer cortex; (*d*) **vascular bundles** of the central cylinder less uniform in transverse view than those of the cortex, and sheathed by parenchyma only or by mechanical tissue always less well developed than that around the cortical bundles.

(i) *Aerial stems* (Ravenala *and* Strelitzia *spp.*). Superficial layers often sclerotic. Cortex narrow. Endodermis absent. Boundary between cortex and central cylinder indicated by a sclerotic ring containing numerous vascular bundles with massive fibrous sheaths. Course of bundles in the stem ± vertical, regular. Ground parenchyma in central cylinder of *Ravenala* becoming aerenchymatous by secondary expansion.

(ii) *Underground stems* (Heliconia, Musa, Orchidantha *and* Strelitzia *spp.*). Superficial layers never thick-walled. Cortex wide. Endodermis present at the boundary between the cortex and central cylinder. Irregular plexus of vascular tissue immediately within the endodermis. Course of vascular bundles very irregular, oblique or horizontal, due to short internodes.

Root

Often thick, or swollen into storage organs by enlargement of the cortex. Exodermis of ligno-suberized cells at periphery of cortex sometimes exhibiting periderm divisions. Radial **air-canals** present in the inner cortex in all genera except *Strelitzia*. **Stelar structure** normal in *Heliconia* and *Orchidantha*; anomalous in *Musa*, *Ravenala* and *Strelitzia*, with phloem strands and wide vessels occupying the centre of the stele.

Vessels

Generally restricted to the metaxylem of the root, but in *Strelitzia*, present also in the aerial stems; most specialized in *Musa*, the vessel elements in this genus frequently having simple perforation plates in transverse end walls; perforation plates in other genera always scalariform, in oblique end walls; vessel elements resembling tracheids in *Orchidantha*.

Stegmata, silica, crystals, tannin and starch

Stegmata present in longitudinal files adjacent to the bundle-sheaths in all parts except the roots; small, with unevenly thickened walls in *Heliconia*, *Musa* and *Orchidantha*; containing silica-bodies with a distinctive shape for each genus (see Appendix A), apart from being alike in *Ravenala* and *Strelitzia*. Silica-bodies also present in unthickened parenchymatous cells (not true stegmata according to S. & M.) in *Ravenala* and *Strelitzia*. Silica-cells of two types noted in *Musa*, and silica-bodies associated with the transverse veins in *Musa*, *Ravenala* and *Strelitzia*.

Groups of rhombohedral **crystals** of calcium oxalate common in all parts, but particularly associated with the assimilatory tissue. Crystal-sand sometimes developed. Raphide sacs common in all parts, usually situated between the palisade and spongy tissue in the lamina, commonly attached to diaphragms in the air-canals of the leaf stalk, and scattered in the ground parenchyma of stem and root.

Tannin generally present in morphologically unspecialized cells in all parts, but not conspicuous in *Orchidantha*. **Laticifers**, containing tannin, associated with the vascular bundles in all organs of *Musa* except the root.

Starch present as grains exhibiting diagnostic shapes for each genus; flattened in

Musa and *Ravenala*; cylindrical in *Heliconia*; angular in *Orchidantha*; spherical (?) in *Strelitzia*; most common in storage rhizomes, stems or fleshy roots, but also present elsewhere, e.g. in the petiole of *Orchidantha*.

ANATOMY OF INDIVIDUAL GENERA

In order to prevent my main thesis from being obscured by a wealth of detail, the anatomy of the individual genera is dealt with as Appendix A on pp. 791–807.

TAXONOMIC CONCLUSIONS DRAWN FROM THE ANATOMICAL DATA

(i) *Specific differences*

In those genera in which more than one species has been examined it is at once obvious that anatomical differences between different species of the same genus are small or absent. Thus species within the genus *Musa* are almost identical anatomically although they may show small differences of cell size. In the material of *Heliconia* which has been examined slight qualitative differences may be present which, if constant, may be diagnostic of the species concerned. For instance, a papillate epidermis is present adaxially in *H. metallica*; *H. psittacorum* and *H. rostrata* have a uniform distribution of stomata in the intercostal regions of the abaxial epidermis which distinguishes them from other species in which the stomata are situated in short, rectangular areas in the intercostal bands; *H. rostrata* has linear walls to the cells of the adaxial epidermis in contrast to other species which have undulate walls. There is some variation in the distribution of fibres and sclerotic tissue in the leaf stalk which could be used to distinguish different species.

However, in spite of this, the range of variations of anatomical structure within a genus is very small compared with the large differences which exist between different genera. Since there is no overlap of anatomical features between one genus and another, the isolation of the genera is particularly emphasized.

Table 3. *Anatomical differences between* Orchidantha *and other members of the Musaceae*

Orchidantha	Other genera
Abaxial epidermis not differentiated into costal and intercostal bands	Abaxial epidermis always differentiated into costal and intercostal bands
Guard cells with conspicuous median wall thickenings	Guard cells not so thickened
Terminal subsidiary cells not differentiated from other epidermal cells	Terminal subsidiary cells often shorter than other epidermal cells
Non-vascular fibres present in lamina	Non-vascular fibres absent from lamina
Palisade absent	Palisade always very distinct
Assimilating tissue made up of large and small cells	Assimilating tissue not so differentiated
Longitudinal veins remote from each other	Longitudinal veins close to each other
Longitudinal veins situated adaxially, never buttressed to the abaxial hypodermis	Longitudinal veins situated at a median depth, often buttressed to the abaxial hypodermis
Parenchyma sheath of longitudinal veins always 1-layered	Parenchyma sheath of longitudinal veins often 2–3-layered
Transverse veins situated abaxially, sheathed by fibres	Transverse veins situated at a median depth, never sheathed by fibres
Bands of expansion cells not visible in mature leaves	Bands of enlarged expansion cells in certain regions of the mature leaf
Silica-bodies ‘hat-shaped’	Silica-bodies never ‘hat-shaped’
Starch grains ± isodiametric, centric, surface with facets	Starch grains eccentric, or smoothly spherical (*Strelitzia*)
Chlorenchyma of leaf stalk diffuse, ground tissues never sclerotic	Chlorenchyma of leaf stalk limited to a distinct band, ground tissues often sclerotic

(ii) *The taxonomic position of* Orchidantha

Recent workers (Hutchinson, 1934; Nakai, 1948; Lane, 1955) have placed *Orchidantha* in its own family, the Lowiaceae, because it possesses a combination of morphological features not found in any other members of the Musaceae. Its general habit, leaf venation, inflorescence structure and floral arrangement distinguish it clearly from its supposed congeners. This isolation is amply supported by anatomical evidence, and, in fact, *Orchidantha* possesses many structures not found in other members of the Musaceae. Table 3 summarizes the more outstanding anatomical features which isolate *Orchidantha*.

(iii) *Affinities of* Ravenala *and* Strelitzia

It is evident from Tables 1 and 2 on pp. 780 and 782 that *Ravenala* and *Strelitzia* are very similar morphologically and they have always been considered to be closely related by taxonomists. This affinity is also supported by anatomical evidence because the two genera bear a combination of anatomical features set out in Table 4.

Table 4. *Anatomical features which distinguish* Ravenala *and* Strelitzia *from other members of the Musaceae*

Ravenala, Strelitzia	Other genera
Stomata sunken	Stomata superficial
Terminal subsidiary cells always distinct, short; other epidermal cells adjacent to the stomatal apparatus modified	Terminal subsidiary cells may or may not be distinct; other epidermal cells adjacent to the stomatal apparatus not usually modified
Abaxial hypodermal cells arranged concentrically around substomatal chambers	Abaxial hypodermal cells not arranged concentrically around substomatal chambers; angular
Adaxial hypodermis always several- (up to 6) layered	Adaxial hypodermis one-layered, or 1–3-layered in *Musa* spp.
Conspicuous fibre buttresses connect longitudinal veins to each hypodermis	Fibre buttresses generally absent, but present in *Musa*
All transverse septa contain vascular tissues	Transverse septa absent, or, if present, mostly without vascular tissue (*Musa*)
Silica-bodies druse-shaped	Silica-bodies never druse-shaped
Silica-cells parenchymatous, thin-walled (false stegmata)	Silica-cells small, with one wall thickened (true stegmata)
Silica-cells comparable to those adjacent to the longitudinal bundles also situated beside the transverse bundles	Silica-cells absent beside the transverse bundles or, if present, usually different from those adjacent to the longitudinal bundles (*Musa*)
Leaf stalk with numerous arcs of air-canals	Leaf stalk with few arcs of air-canals
Adaxial vascular and fibre tissue absent from leaf stalk	Adaxial vascular and fibre tissue present in leaf stalk
Transverse diaphragms of air-canals of leaf stalk never 1-layered	Transverse diaphragms often 1-layered
Chlorenchyma situated abaxially in the leaf stalk	Chlorenchyma band situated adaxially, or absent (*Orchidantha*)
Stem often an erect, woody trunk, the endodermis and vascular plexus then being absent	Stem always underground; endodermis and vascular plexus present
Stelar structure of root anomalous, central phloem strands contain only one sieve-tube	Stelar structure of root normal, or, if anomalous (*Musa*), the central phloem strands contain many sieve-tubes

From Tables 4 and 5 it is evident that *Strelitzia* and *Ravenala* together share several common features with *Musa*. Thus in the development of the adaxial hypodermis, the structure of the longitudinal and transverse veins, the distribution of silica and in the presence of anomalous root structure, *Musa* bears some resemblance to *Ravenala* and *Strelitzia*. Also the starch grains are flattened in all three genera. However, these similarities cannot be regarded as important since *Musa* shows many structures which readily distinguish it from *Ravenala* and *Strelitzia*.

There do not seem to be many important anatomical differences between *Ravenala* and *Strelitzia*. It may be noted, however, that *Strelitzia*, unlike *Ravenala*, has no air-canals in its roots; *Strelitzia* has a cuticle of rod-like particles on the abaxial surface of the lamina, whereas in *Ravenala*, the cuticle is uniform. The starch grains of *Ravenala* are flattened, those of *Strelitzia* appear to be spherical. The two genera are probably best distinguished by differences in the number of air-canals in the leaf stalk (cf. Figs. 37 and 60). Vessels are present in the aerial stems of *Strelitzia*, but none have been seen in *Ravenala*. However, I am still not certain that vessels are absent from the aerial stem of *Ravenala*, because the tracheal elements in the stem are very long, so that unbroken elements can never be isolated by maceration and no definite end wall has yet been observed.

According to Lane (1955), *Phenakospermum* is more closely related to *Strelitzia* than to *Ravenala*. In the absence of vegetative material of *Phenakospermum* for anatomical study anatomical support for this scheme is not available.

(iv) *Affinities of* Musa

Musa has a combination of anatomical characters which makes it readily distinguishable from other genera and indeed *Musa* has several unique structures. These are outlined in Table 5.

Table 5. *Anatomical features which distinguish* Musa *from other Musaceae*

Musa	Other genera
Spongy mesophyll replaced by air-canals alternating with the longitudinal veins	Spongy mesophyll developed normally
Transverse parenchymatous septa in mesophyll at frequent intervals	Parenchymatous septa absent
'Pulvinar band' differentiated at junction of midrib and lamina	'Pulvinar band' not obvious
Silica-cells of two types in the lamina	Silica-cells of one type only in the lamina
Silica-bodies 'trough-shaped', each with a shallow depression	Silica-bodies not 'trough-shaped', except in *Heliconia* where the depression is very deep
Laticifers associated with vascular bundles	Laticifers absent
Leaf stalk contains a single arc of air-canals at all levels; air-canals never adaxial to main vascular bundle arc	Leaf stalk with more than one arc of air-canals at certain levels; air-canals adaxial to main vascular arc in midrib and petiole
Phloem strands at centre of root stele with several sieve tubes	Phloem strands either absent from centre of stele, or containing only one sieve tube

Table 6. *Anatomical features diagnostic of* Heliconia

Heliconia	Other genera
Anticlinal walls of epidermal cells undulate	Walls of epidermal cells linear
Hypodermis beneath each surface always 1-layered	Hypodermis below the adaxial surface often more than 1-layered
Longitudinal veins fairly remote from each other	Longitudinal veins generally close together, but very remote in *Orchidantha*
Longitudinal veins situated at a median depth, without conspicuous buttresses	Longitudinal veins generally with conspicuous buttresses, or, in *Orchidantha* veins more adaxial and not buttressed
Transverse veins never buttressed; sheathed by parenchyma cells and never by fibres	Transverse veins either buttressed or sheathed by fibres
Abaxial hypodermis of thin-walled cells differentiated in leaf stalk	Abaxial hypodermis sclerotic or not differentiated from other ground tissue cells in the leaf stalk
Silica-bodies 'trough-shaped' each with a deep central depression	Silica-bodies either not 'trough-shaped', of if 'trough-shaped' (*Musa*) with a shallow central depression
Starch grains cylindrical, ellipsoidal, never flattened	Starch grains flattened, or ± isodiametric

(v) *Affinities of* Heliconia

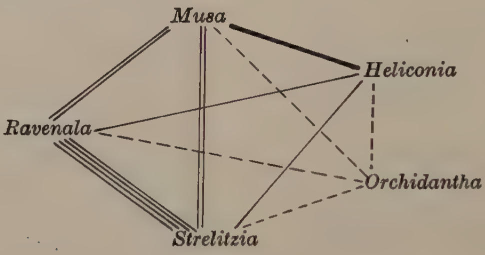
Heliconia can be readily distinguished anatomically from the other genera of Musaceae by the features summarized in Table 6. *Heliconia* resembles *Musa* in having an adaxial band of chlorenchyma in the leaf stalk, and also the silica-bodies in the two genera are very similar although they differ in the depth of the central depressions which they bear. These similarities cannot be regarded as important, however, and there is no other evidence that *Heliconia* is more nearly allied to *Musa* than to the other genera of the family. Similarly, *Heliconia* resembles *Orchidantha* in the way in which the lamina veins are distributed, but these similarities are quite unimportant.

(vi) *General conclusions*

From the anatomical observations which have been presented in this paper, the following scheme could be used to express the relationships between the main genera of the Musaceae:

Orchidantha
{ *Musa*
{ { *Ravenala*
{ { *Strelitzia*
{ *Heliconia*

This is represented diagrammatically below:



Diagram

Comparing these results with those expressed in Table 2 it is evident that they show most agreement with the views of Lane (1955). He emphasized the distinctiveness of *Orchidantha* by placing it in its own family. Within his Musaceae, *Heliconia* is separated from the other genera by virtue of its being placed in its own subfamily, the Heliconioideae. Unfortunately, Lane places the three remaining genera together in the same subfamily, the Musoideae, and does not emphasize the fact that *Strelitzia* and *Ravenala* are much more closely related to each other than they are to *Musa*. Neither Hutchinson (1934) nor Nakai (1948) indicate that *Orchidantha* is isolated from the other members of the group, because *Musa*, *Ravenala*, *Strelitzia* and *Heliconia* are treated so that more than one family is created out of them. Hutchinson places *Heliconia* with *Strelitzia* and *Ravenala* in the Strelitziaceae, although it is not apparent that *Heliconia* is more closely related to these two genera than it is to *Musa*. In fact, the available evidence suggests that the converse is nearer the truth. Nakai does emphasize the isolation of *Heliconia*, but in creating the three families Musaceae, Strelitziaceae and Heliconiaceae he obscures the fact that the genera contained in them are more closely related to each other than they are to *Orchidantha*.

APPENDIX A

ANATOMY OF THE INDIVIDUAL GENERA OF MUSACEAE

(1) Musa

Lamina

Leaf dorsiventral. **Cuticle** of rod-like particles perpendicular to the surface, and forming a bloom on the abaxial surface of young leaves. **Hairs** absent. **Epidermis**; adaxial epidermis uniform (Fig. 1); cells in fairly regular but discontinuous files, the cells themselves being rectangular, always longitudinally extended, with anticlinal walls linear in surface view; abaxial epidermis (Fig. 2) differentiated into narrow costal, and wide intercostal, bands; cells of costal regions narrow and elongated, the intercostal cells being slightly bigger and very irregular. Epidermal cells sometimes papillate, e.g. in *M. sumatrana* and *M. basjoo*; cells on both surfaces with the outer tangential walls only slightly thickened and the others thin. **Stomata** few to many on the adaxial, but always much more numerous on the abaxial, surface; uniformly distributed within each abaxial intercostal region and not in clearly defined files; 24·0–33·0μ long; terminal subsidiary cells (Fig. 3) short, never papillose; guard cells not markedly sunken, with walls scarcely thickened (Fig. 4). **Hypodermis**; adaxial 1–2-layered, abaxial 1-layered; cells of the adaxial hypodermis in distinct longitudinal files, individual cells being transversely extended (Fig. 6) and often hexagonal in surface view; cells of the abaxial hypodermis not in distinct files, very irregular in shape and smaller than those of the adaxial hypodermis. **Mesophyll** (Fig. 7) with 2–3 layers of very distinct palisade cells; spongy tissue replaced by longitudinal **air-canals** alternating with the vascular bundles and each lined by an irregular layer of small chlorenchyma cells, long-armed cells extending across the canals at intervals. Air-canals traversed at intervals by **transverse septa**, each septum consisting of compact, colourless, tranversely extended, interlocking, parenchymatous cells (Fig. 9) and occasional thick-walled cells, intercellular pores through the septa being either absent or small.

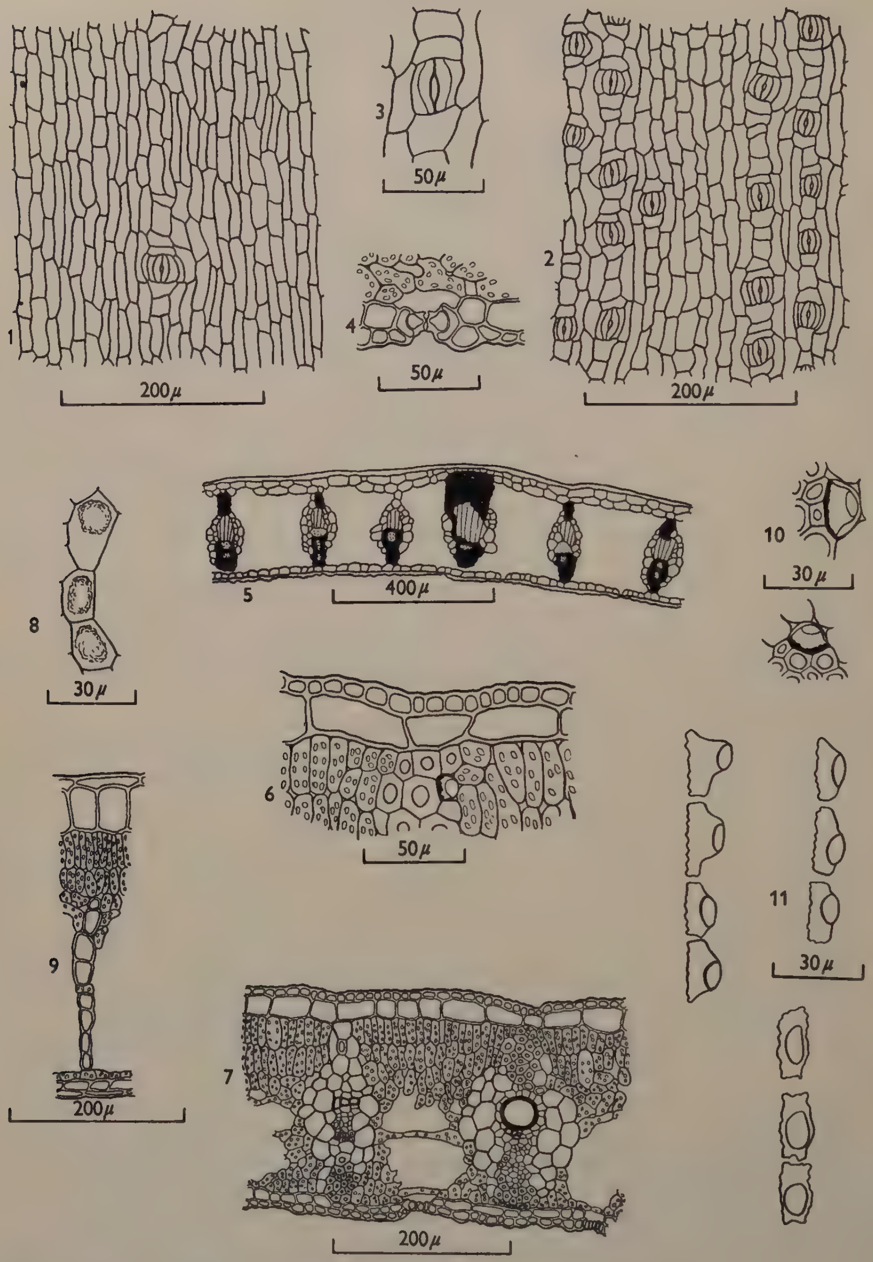
Longitudinal veins (Fig. 5) embedded in girders (buttresses) of tissue extending from the adaxial to the abaxial hypodermis, the abaxial part of each girder usually consisting of fibres and the adaxial part either of fibres or parenchyma; assimilatory tissue sometimes present above or below a vascular bundle. Vascular bundles each with a parenchymatous bundle-sheath, usually 2–3 cells wide at the sides of the veins. Phloem sclerotic in *M. sumatrana*. Transverse **vascular commissures** extending across the transverse parenchymatous septa connect the longitudinal vascular bundles to one another at irregular intervals. **Expansion cells** present in association with each of the main lamina bundles near enlarged portions of the adaxial hypodermis. Diurnal movements of the lamina effected by a 'pulvinar band' (Skutch, 1927) at the junction between the lamina and midrib, air-canals being absent from this position, and with very numerous vascular bundles having thick sclerotic sheaths, the abaxial hypodermis being enlarged and the adaxial cuticle attached to the epidermis by pegs.

Midrib, petiole and leaf-sheath (Figs. 12–16)

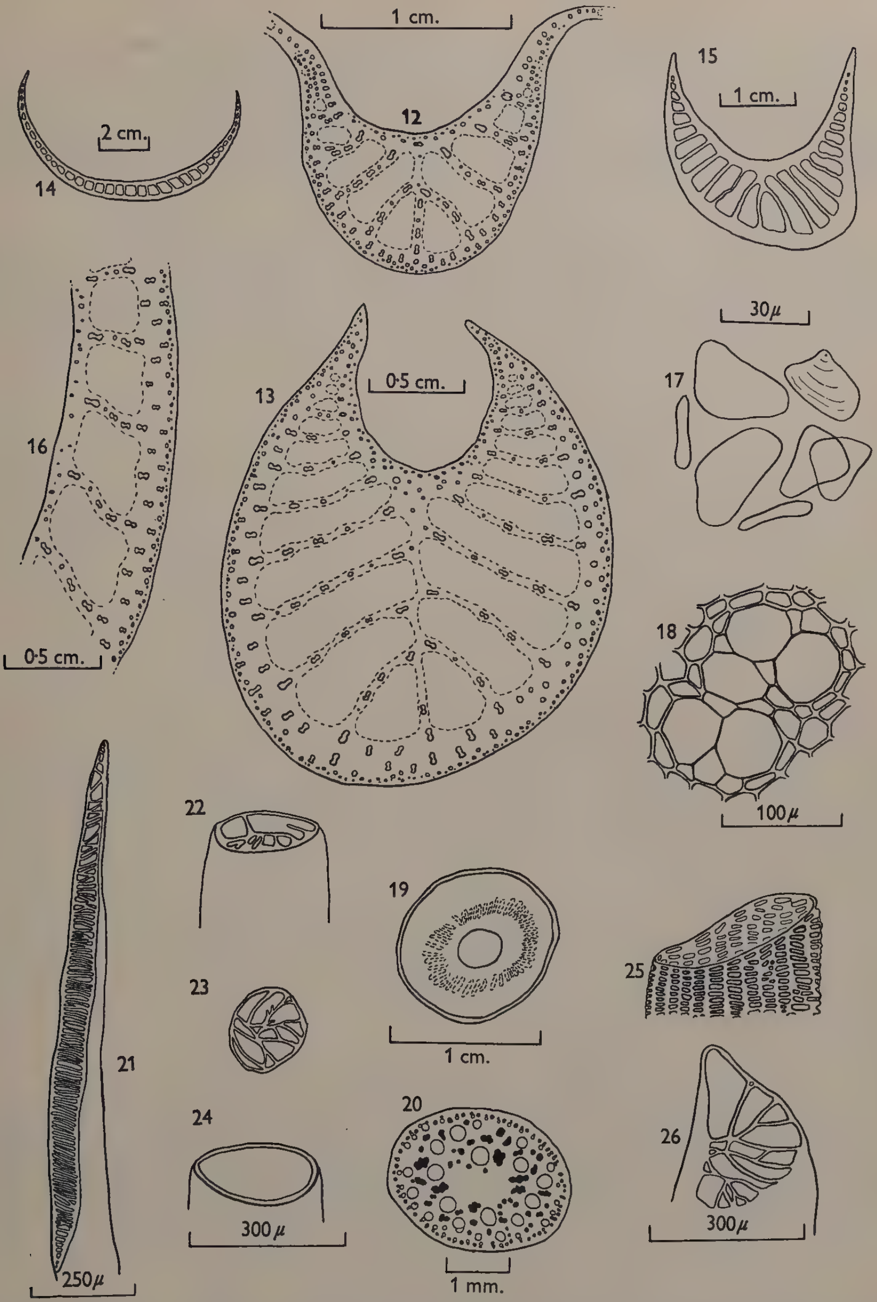
Air-canals arranged in a single arc at all levels, the canals being traversed at intervals by transverse diaphragms. **Diaphragms** either each consisting of a single layer of stellate parenchyma, or of several cell layers, only certain of these being stellate.[1] Small adaxial fibre strands and vascular bundles present at all levels. **Chlorenchyma** forming an abaxial band in the midrib and petiole. Abaxial **hypodermis** of midrib and petiole sclerotic;[2] adaxial hypodermis sometimes slightly sclerotic in the petiole. Numerous small depressions or '**pits**' (Skutch, 1927) present in the adaxial surface of the sheath. Stomata sometimes present in the depressions but not confined to them.

[1] Skutch describes two types of diaphragm in the sheath of the Gros Michel banana—single-layered and three-layered, the centre layer of the latter composed of rounded cells. According to S. & M. and my own observations the state of affairs appears to be less precise than this.

[2] According to Skutch (1927) sclerosis of the abaxial hypodermis of the leaf sheath only occurs in the outermost sheaths of the pseudostem and may be due to the influence of light. Sclerosis always begins in the hypodermal cells surrounding substomatal chambers.



Figs. 1–26. Anatomy of *Musa*. 1. Adaxial epidermis, surface view (*M.* '*sapientum*', W. Africa). 2. Abaxial epidermis, surface view (*M.* '*sapientum*', W. Africa). 3. Stoma, surface view, abaxial epidermis (*M.* '*sapientum*', W. Africa). 4. T.S. stoma, abaxial epidermis (*M. sumatrana*). 5. T.S. lamina, mechanical tissue (solid black), xylem (lined), phloem (stippled) (*M. sumatrana*). 6. T.S. adaxial surface layers (*M. malaccensis*). 7. T.S. lamina, including a main vein (*M.* '*sapientum*' Hort., Kew). 8. Silica-cells from transverse septum of lamina (*M.* '*sapientum*' Hort., Singapore). 9. L.S. lamina, transverse septum in T.S. (*M. sumatrana*). 10. T.S. part of fibre buttress of lamina showing stegmata (*M.* '*sapientum*' Hort., Singapore). 11. Silica-bodies from lamina (*M. basjoo* and *M.* '*sapientum*' Hort., Singapore). 12. T.S. midrib, halfway between its



base and apex (*M.* '*sapientum*', W. Africa). 13. T.S. petiole, just below insertion of lamina (*M.* '*sapientum*', W. Africa). 14. Outline T.S. lower part of leaf sheath (*M.* '*sapientum*', W. Africa). 15. Outline T.S. upper part of leaf sheath (*M.* '*sapientum*', W. Africa). 16. T.S. lateral part of leaf sheath (*M.* '*sapientum*', W. Africa). 17. Starch grains from rhizome (*M.* '*sapientum*', W. Africa). 18. Phloem island from centre of stele of root (*M.* '*sapientum*' Hort., Singapore). 19. Outline T.S. of root (*M.* '*sapientum*' Hort., Singapore). 20. T.S. stele of root showing distribution of phloem (solid black) and xylem (open circles) (*M.* '*sapientum*' Hort., Singapore). 21–26. End walls of vessel elements from a single root, showing range of variation. Only in 25 is the pitting on the lateral walls represented (*M.* '*sapientum*', W. Africa).

Stem (based on its description by Skutch, 1932)

Vegetative axis consisting of a thickened, underground, corm-like structure, with short internodes. **Periderm** sometimes arising in the outer cortex. **Cortex** delimited from the central cylinder by an **endodermis** and 'secondary' bundle plexus. Course of the vascular bundles very irregular, a distinct cortical bundle system being present. Bundles of the central cylinder, unlike those of the cortex, not provided with fibrous sheaths. Leaf traces amphiphloic for part of their course.

Root (Figs. 18–20)

Never swollen into a storage organ. **Periderm** sometimes arising in the outer cortex. Radial **air-canals** conspicuous in the inner cortex. **Stelar structure** anomalous, with wide vessels and irregular phloem islands scattered throughout the ground tissue of the stele. Phloem islands containing many large sieve tubes (Fig. 18) cf. *Ravenala* and *Strelitzia*.

Metaxylem vessels and phloem

Metaxylem vessels confined to the root; 100–350μ in diameter; elements up to 6270μ long with simple perforation plates on transverse end walls (Figs. 24, 25), or with scalariform perforation plates on slightly oblique or oblique end walls (Fig. 21), the thickening bars being few or many; other elements with reticulate perforation plates on transverse or slightly oblique end walls (Figs. 22, 23 and 26). All of these types occurring together in a single root.

Sieve tubes in the phloem islands of the root with simple sieve plates on transverse end walls. Simple sieve plates also recorded by S. & M. in the root.

Stegmata, silica-bodies, crystals, starch, tannin and laticifers

(i) **Stegmata** (Figs. 6, 8, 10 and 11) present in longitudinal files adjacent to the fibrous portions of the bundle-sheaths in the lamina (Figs. 6, 10), and less frequently in the corresponding position in the leaf stalk, the walls of the silica-cells adjacent to the fibres being slightly thickened and pitted. Silica-bodies in the stegmata (Fig. 11) more or less rectangular, 'trough-like' (S. & M.) and each with a central depression away from the fibres, the spinous bases of the bodies being said to project into pits in the thickened parts of the walls. (ii) Spherical silica-bodies, each with a granulose surface, also present but situated in small, unthickened cells adjacent to the parenchymatous sheaths of the vascular bundles of leaf and stem, and frequent in the cells of the transverse septa of the lamina (Fig. 8). Silica-bodies in these cells stated by Skutch (1927) to be attached to the cell walls by short stalks. Silica completely absent from the roots.

Crystals of calcium oxalate present as abundant rhombohedra in all parts, and sometimes forming a coarse sand; raphide sacs numerous.

Starch grains (Fig. 17) flattened, eccentric. **Tannin** ubiquitous in morphologically unspecialized cells. **Articulate laticifers** associated with the vascular bundles of all organs except the root (Skutch, 1932), the mucilaginous contents of these elements exuding at cut surfaces and darkening on exposure to air. Laticifers and tannin cells difficult to distinguish in transverse sections. Schizogenous **mucilage cavities**, apparently containing the same material as the laticifers, recorded in the phloem of *Musa* by Skutch (1930).

(2) Ensete

Scarcely distinguishable anatomically from *Musa*. **Stomata** almost equally numerous on both surfaces of the lamina, 29·5–37·5μ long; parenchymatous bundle-sheaths very conspicuous in *Ensete gilletii*. **Stegmata** in this species with silica-bodies all of type (ii) described above for *Musa*; 'trough-shaped' bodies absent. Silica-bodies intermediate between types (i) and (ii) in *E. arnoldianum*. Radial **air-canals** in the root very small. **Vessel elements** 43–115μ in diameter and 1585–3890μ long.

(3) Ravenala (*including* Phenakospermum)

Lamina

Leaf dorsiventral. **Hairs** absent. **Epidermis** with cell walls wholly cutinized; cuticle on the abaxial surface thick and cracking in mature leaves. Adaxial epidermis (Fig. 27) uniform, cell files distinct but short and rather irregular; cells ± rectangular and elongated, but often isodiametric or very short and somewhat larger than those of the abaxial epidermis, walls ± linear. Abaxial epidermis (Fig. 28) differentiated into narrow costal, and fairly wide intercostal, bands; cells of costal bands in distinct files, narrow, elongated, rectangular; cells in the intercostal regions not arranged in distinct files, very irregular. Outer tangential walls of the cells of each epidermis slightly thickened, remaining walls scarcely thicker than those of the mesophyll cells. **Stomata** infrequent on the adaxial surface; in intercostal regions of the abaxial surface absent below the transverse commissures and therefore limited to rectangular areas; length $28{\cdot}0\mu$. Stomata not in regular files; accompanied by very distinct, wide and short terminal subsidiary cells; other cells adjacent to the stomatal apparatus sometimes modified (Fig. 30). Stomata (Fig. 32) sunken in depressions, often surrounded by ridges of cuticle; guard cells without special thickenings.

Hypodermis 3–4-layered on the adaxial, and 2-layered on the abaxial, surface (Figs. 29, 34). Adaxial hypodermal cells (Figs. 33–35) in distinct longitudinal files, the outermost layer consisting of transversely extended cells, hexagonal in surface view; cells of the inner layers cubical, the lowest layer often containing anticlinally extended cells protruding into the palisade; costal regions often distinguished by small, cubical, hypodermal cells. Cells of the abaxial much smaller than those of the adaxial hypodermis, and not arranged in distinct longitudinal files except in the costal regions, those of the intercostal regions being very irregular in shape and size. A single ring-shaped cell, or 2–3 of the innermost cells, encircle the substomatal chambers of the abaxial region. **Mesophyll** with 2–4 layers of palisade cells (Fig. 34), the uppermost layer often being interrupted by large, colourless hypodermal cells; spongy tissue made up of loosely arranged cells with short arms. **Vascular bundles** of the longitudinal veins sheathed laterally by 1–2 layers of elongated parenchymatous cells, vertical extensions of the sheaths, resembling buttresses, connecting the bundle-sheaths to each hypodermis (Fig. 29). **Transverse commissures**, sheathed by slightly thick-walled cells and with vertical extensions of interlocking parenchymatous cells connecting them to the palisade and to the abaxial hypodermis, and thus forming complete septa in the spongy mesophyll (Fig. 35). Parenchymatous septa, devoid of vascular tissue, absent. **Expansion cells** often forming bands above the main lateral veins of the lamina, the hypodermis being considerably enlarged. Differing from *Musa* in the lack of a 'pulvinar band', but with the adaxial hypodermis enlarged at the junction of the lamina and midrib and abruptly demarcated from the hypodermis of the midrib.

Midrib, petiole and leaf-sheath (Figs. 36–41)

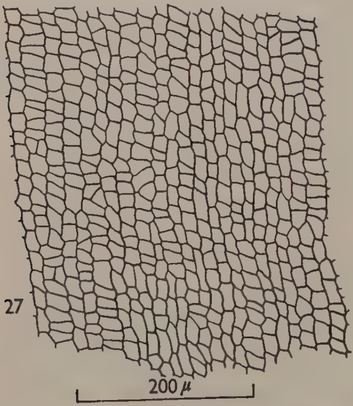
Notable characters include the lack of fibres and vascular bundles above the main arc of longitudinal vascular bundles; the numerous arcs of **air-canals**, some being adaxial to the main arc in the midrib and petiole; the adaxial **hypodermis** of transversely extended, sclerotic cells; the sclerotic abaxial hypodermis, the cells being especially thickened in the leaf-sheath and at the base of the petiole; the thin-walled cells interrupting the sclerotic hypodermis below the stomata; the **chlorenchyma** subjacent to the abaxial surface at all levels.

Aerial stem

Consists of an erect, woody trunk. **Periderm** not observed. **Cortex** narrow, devoid of fibre strands; outer layers heavily sclerosed in mature stems. **Endodermis** absent, but cortex separated from the central cylinder by a sclerotic, parenchymatous cylinder with numerous vascular bundles, each strongly sheathed by fibres, embedded in it. **Vascular bundles** of the central cylinder varying in appearance in transverse sections owing to frequent anastomoses, each bundle being completely encircled by a sheath of 3–5 layers of slightly thickened, parenchymatous cells; cortical bundles sheathed by fibres next to the phloem and by slightly thickened parenchymatous cells next to the xylem. Secondary increase in stem girth allowed for by the formation of lacunae between the vertical walls of the cells of the ground tissue, the cells themselves becoming transversely stretched and sometimes stellate or long-armed.

Root

(*a*) Subterranean roots characterized by (i) a cortex with the outer cell layers suberized or lignified; (ii) very conspicuous, radial air-canals (Fig. 42); (iii) a stele with very wide vessels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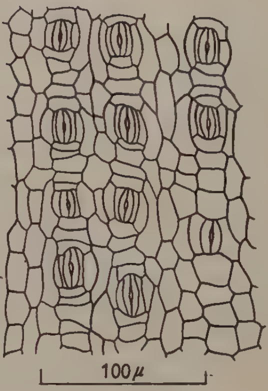
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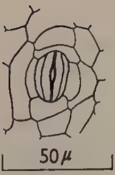
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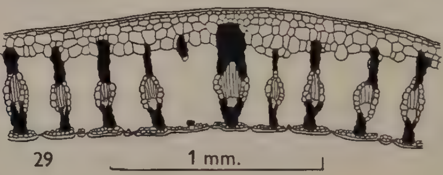
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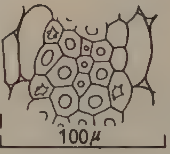
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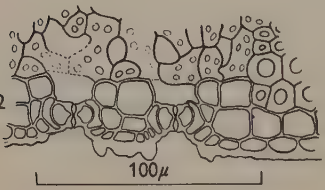
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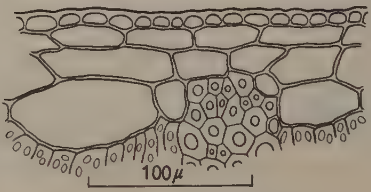
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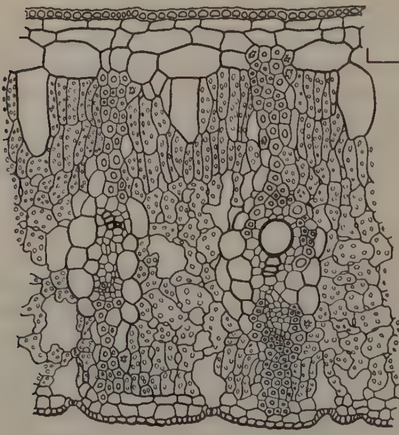
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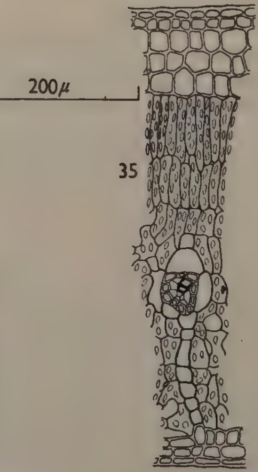
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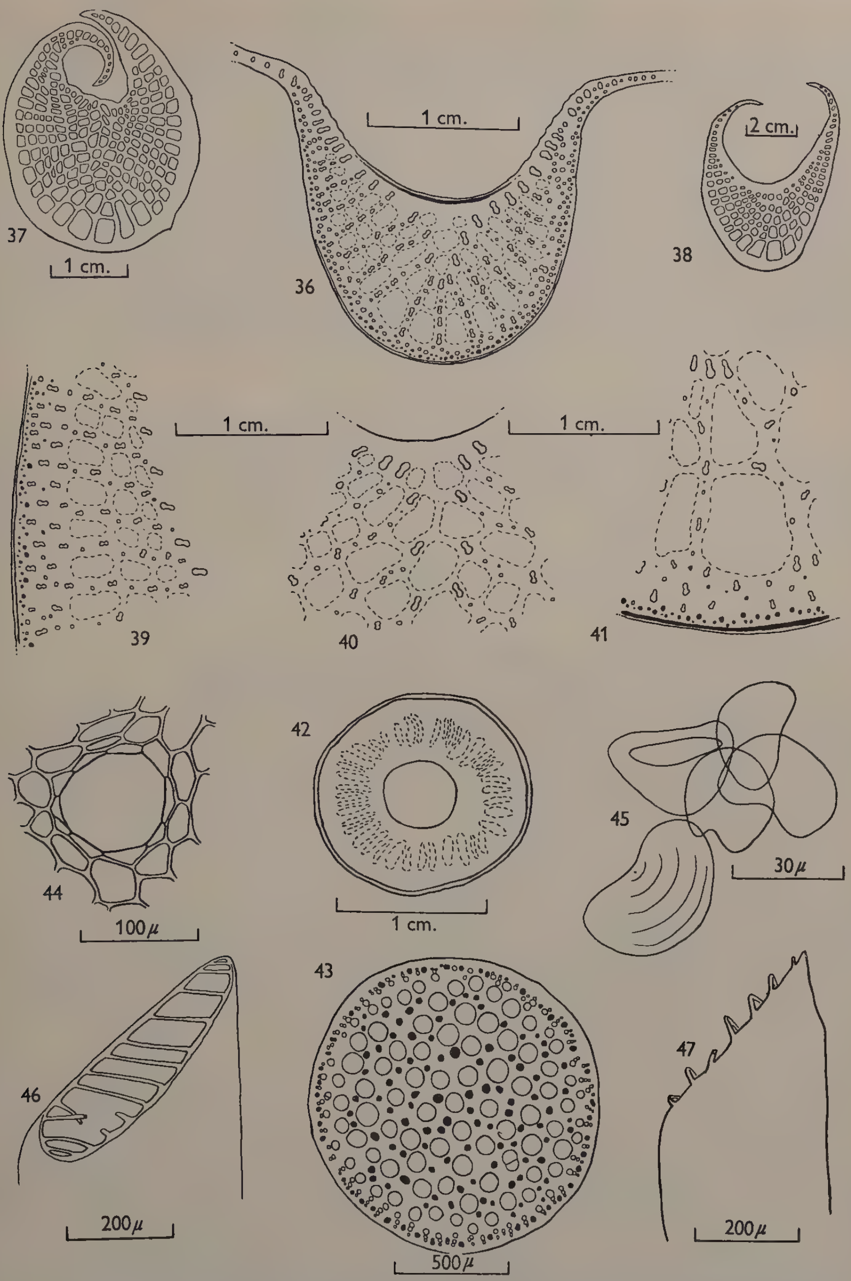


Figs. 27–47. Anatomy of *Ravenala* (*R. madagascariensis*). 27. Adaxial epidermis, surface view. 28. Abaxial epidermis, surface view. 29. T.S. lamina, mechanical tissue (solid black), xylem (lined), phloem (stippled). 30. Stoma, surface view, abaxial epidermis. 31. T.S. fibre buttress in lamina with associated silica-cells. 32. T.S. abaxial surface layers of lamina. 33. T.S. adaxial surface layers of lamina. 34. T.S. lamina, including a large vein. 35. L.S. lamina showing a transverse commissure in T.S. 36. T.S. midrib halfway between its base and apex. 37. T.S. petiole, showing distribution of air-canals only. 38. T.S. upper part of leaf sheath showing distribution of air canals only. 39. Enlargement of lateral part of 38. 40. Enlargement of adaxial part of 38. 41. Enlargement of abaxial part of 38. 42. Outline T.S. of root. 43. T.S. stele of root, showing distribution of phloem (solid black) and xylem (open circles). 44. Phloem island from centre of stele. 45. Starch grains from stem. 46 and 47. End walls of vessel elements in root.

and small phloem strands scattered throughout the ground parenchyma (Fig. 43), each phloem island containing a single sieve tube surrounded by thin-walled parenchyma (Fig. 44).

(*b*) Aerial roots (from Singapore) distinguished by having protective layers of thick-walled cells; no air-canals; normal stelar structure.

Stegmata, crystals, tannin, laticifers and starch grains

Stegmata (not regarded as true stegmata by S. & M.) present as longitudinal files of silica-cells adjacent to the vascular bundles of all organs except the root. Silica-cells very abundant in the parenchyma of the transverse septa, each cell more or less isodiametric or elongated, with unthickened walls, and containing a spherical and stellate, or druse-like, silica-body, often accompanied by silica sand. **Crystals** of calcium oxalate, including raphides, present as in *Musa*. **Tannin cells** with dark contents, present in all parts. **Laticifers** absent. **Starch grains** (Fig. 45) flattened and eccentric, as in *Musa*, but usually kidney-shaped.

Vessels and sieve tubes

Vessels (Figs. 46, 47) confined to the root metaxylem; elements 96–310μ in diameter and 1900–5000μ long; perforation plates always scalariform, but usually with few bars, and slightly oblique to oblique. Sieve tubes from the phloem strands in the root with compound sieve plates on long end walls.

(4) Strelitzia

Lamina

Leaf dorsiventral. **Hairs** absent. **Epidermis** wholly cutinized; cuticle, as in *Musa*, with rod-like particles producing a waxy bloom on the abaxial surface, the rods often over-arching the stomatal depressions (De Bary, 1884, Fig. 29). Adaxial epidermis uniform (Fig. 48), cells in distinct longitudinal files; individual cells more or less rectangular, usually longitudinally extended, sometimes isodiametric or short; walls linear. Abaxial epidermis (Fig. 49) differentiated into narrow costal, and wide intercostal, regions; costal cells rectangular, elongated and in distinct longitudinal files; intercostal cells variable in shape and in irregular longitudinal files. Cells of the adaxial slightly larger than those of the abaxial epidermis, the cell walls of each epidermis being scarcely thickened, but with the outer tangential walls slightly thicker than the others. **Stomata** infrequent on the adaxial, and restricted to rectangular intercostal areas on the abaxial, surface; not in distinct files; 23·5–35·5μ long; more or less sunken (Fig. 54) guard cells without special thickenings; terminal subsidiary cells short and wide (Fig. 52); other epidermal cells adjacent to the stomatal apparatus also modified. **Hypodermis** (Figs. 50, 56) 3–4-layered (3–6-layered according to S. & M.) adaxially, 1-layered (e.g. *S. reginae*) or 1–2-layered (e.g. *S. nicolai*) abaxially. Cells of the adaxial hypodermis in regular longitudinal files, and square or hexagonal in surface view; innermost cells sometimes anticlinally extended; cells of the outermost layer small and transversely extended. Cells of the abaxial hypodermis small, irregular in shape and not in distinct files except in the costal regions. Substomatal chambers wide, with two to three hypodermal cells arranged concentrically around them. **Mesophyll**; palisade tissue 2–3-layered, very distinct (Fig. 56), but often interrupted by anticlinally extended hypodermal cells, especially above the transverse commissures; spongy tissue either consisting of rounded, compact cells (*S. reginae*) or of loose, lobed, chlorenchyma cells (*S. nicolai*); cells of the most abaxial layer of mesophyll somewhat palisade-like, and more compact than those above. Longitudinal **veins** all connected to each hypodermis by extensions of the bundle-sheaths (Fig. 50) resembling buttresses and consisting of fibres. Parenchyma of the bundle-sheaths 1–2-layered laterally. **Transverse commissures**, sheathed by slightly thick-walled cells (Fig. 57), present in transverse parenchymatous **septa** in the spongy tissue, as in *Ravenala*. **Expansion cells**, as in *Ravenala*, associated with the main lateral veins of the lamina; ‘pulvinar-band’ absent.

Stem

(*a*) *Woody trunk of* Strelitzia nicolai

Cortex narrow; cells of the outer layers with thin, suberized walls; **periderm** subjacent to the outer layers, produced by very active cell division; fibre bundles absent; **vascular**

bundles each with a fibrous sheath, external to the phloem only, the cells adjacent to the xylem being parenchymatous. **Endodermis** absent, but cortex delimited from the central **stele** by a sclerotic ring with numerous vascular bundles with well-developed fibre sheaths embedded in it. Vascular bundles of the central stele irregular and with frequent fusions, the bundle-sheaths being absent or devoid of mechanical tissue. Cells of the ground parenchyma enlarged, but, unlike *Ravenala*, air-canals absent.

(*b*) *Rhizome of* Strelitzia reginae

Differing from the woody trunk of *S. nicolai* in the following respects. **Periderm** and suberized superficial layers absent. **Cortex** wide, containing leaf traces passing obliquely into the central cylinder. **Endodermis** present. **Central cylinder** containing numerous vascular bundles of irregular distribution and variable structure.

Root

Thick and fleshy, with enlarged **cortex** especially in rhizomatous species. **Periderm** divisions in outer cortex of *S. augusta*, but none seen in other species. Outer cortical layers suberized or lignified; thick-walled in *S. nicolai*. Radial **air-canals** absent from inner cortex in all species (Fig. 62). Enlarged, hypertrophied cortical cells observed in *S. nicolai*, *S. parvifolia*. **Pericycle** 2-layered in *S. augusta* and *S. nicolai*; 1–3 layered in *S. nicolai* according to S. & M. **Stele** anomalous, as in *Ravenala*, with numerous central vessels and phloem strands, the latter each containing a single, wide sieve tube with sieve plates similar to those in the sieve tubes of *Ravenala*.

Stegmata, crystals, starch, tannin and laticifers

Stegmata (Figs. 51, 53), similar in type and distribution to those of *Ravenala*; exceptionally abundant in the rhizome of *S. reginae*. S. & M.'s report of silica-bodies in the leaf stalk not confirmed. **Crystals** of calcium oxalate common; raphide sacs numerous. **Tannin**, in morphologically unspecialized cells, common in all parts. **Laticifers** absent. **Starch** in the form of spherical grains noted in the stem of *Strelitzia* sp. from Rhodesia (Fig. 61).

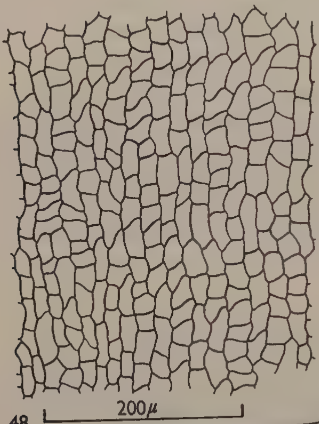
Vessels (Figs. 63–66)

True vessels present in the metaxylem of the root of all species, and also in the erect woody stems of species possessing them. Vessel elements in the root 55–220μ in diameter and 1740–3170μ long, with very long perforation plates on oblique to very oblique end walls (Figs. 64–66); stem vessels (Fig. 63) 80–260μ in diameter and 1210–3335μ long.

(5) Heliconia

Lamina

Leaf dorsiventral. **Hairs** recorded only on the leaf sheath of *H. illustris* (S. & M.); uniseriate, sympodially branched. **Cuticle** thin; consisting of rod-like particles in *H. pulverulenta* (S. & M.); epidermal cells never completely cutinized. **Epidermis**; adaxial epidermis of uniform cells (Fig. 67), arranged in regular files; individual cells ± isodiametric in surface view; cell outlines markedly undulate (except on the adaxial surface of *H. rostrata* cultivated at Kew); cells conspicuously papillate in *H. metallica* (Fig. 72), *H. pulverulenta* (S. & M.), slightly papillate in *H. rostrata*. Abaxial epidermis (Fig. 68) differentiated into costal regions and wider intercostal regions. Cells in costal regions elongated, narrow, otherwise like those of the adaxial epidermis; intercostal cells irregular and not in distinct files. All cells, except the subsidiary cells of the stomata, with undulate walls, but undulations not prominent in *H. rostrata*. Abaxial epidermal cells smaller than those of the adaxial epidermis and never distinctly papillate (Fig. 76). Epidermal cells of both surfaces with unthickened walls. **Stomata** infrequent on or absent from the adaxial surface; abaxial stomata often limited to small rectangular areas in the intercostal regions; those of *H. psittacorum* and *H. rostrata* uniformly distributed in intercostal regions; 24·0–30·5μ long; not in files; with very distinct, short and wide terminal subsidiary cells (Fig. 69). Other epidermal cells adjacent to the stomata sometimes modified, the cells in the same files as the terminal subsidiary cells often being shorter than the rest. Guard cells not sunken, walls not specially thickened (Fig. 71). **Hypodermis** beneath each surface always 1-layered (Figs. 70, 76). Adaxial hypodermal cells in longitudinal files, transversely extended and hexagonal in surface view. Abaxial hypodermal cells always smaller than those of the adaxial hypodermis; intercostal hypodermis interrupted by substomatal chambers, each surrounded by three to four hypodermal cells as in *Musa*. **Mesophyll** with two to three layers of well-differentiated palisade cells (Fig. 76). Spongy tissue consisting of lobed cells in most species (Fig. 76), but more compact and composed of rounded cells in *H. psittacorum* and *H. rostrata*. Abaxial mesophyll compact beneath longitudinal and transverse veins. Non-vascular fibre strands recorded only for *H. illustris* by



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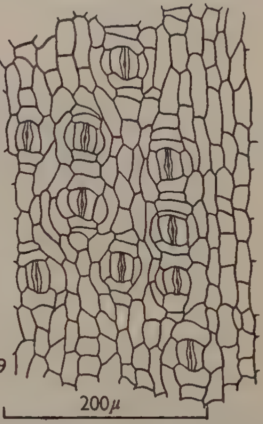

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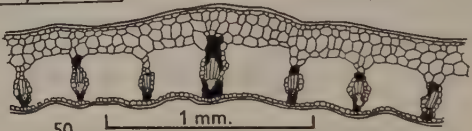

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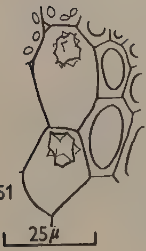

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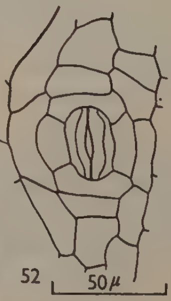

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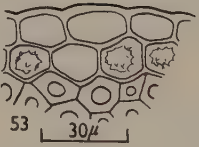

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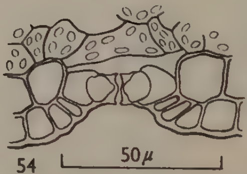

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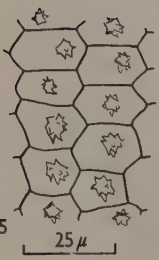

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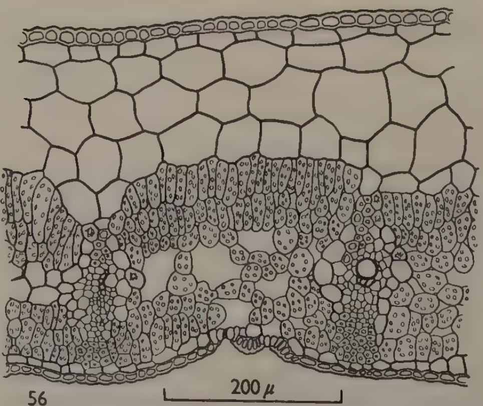

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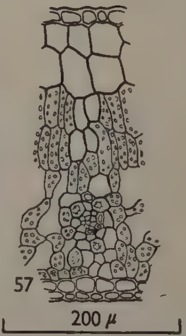

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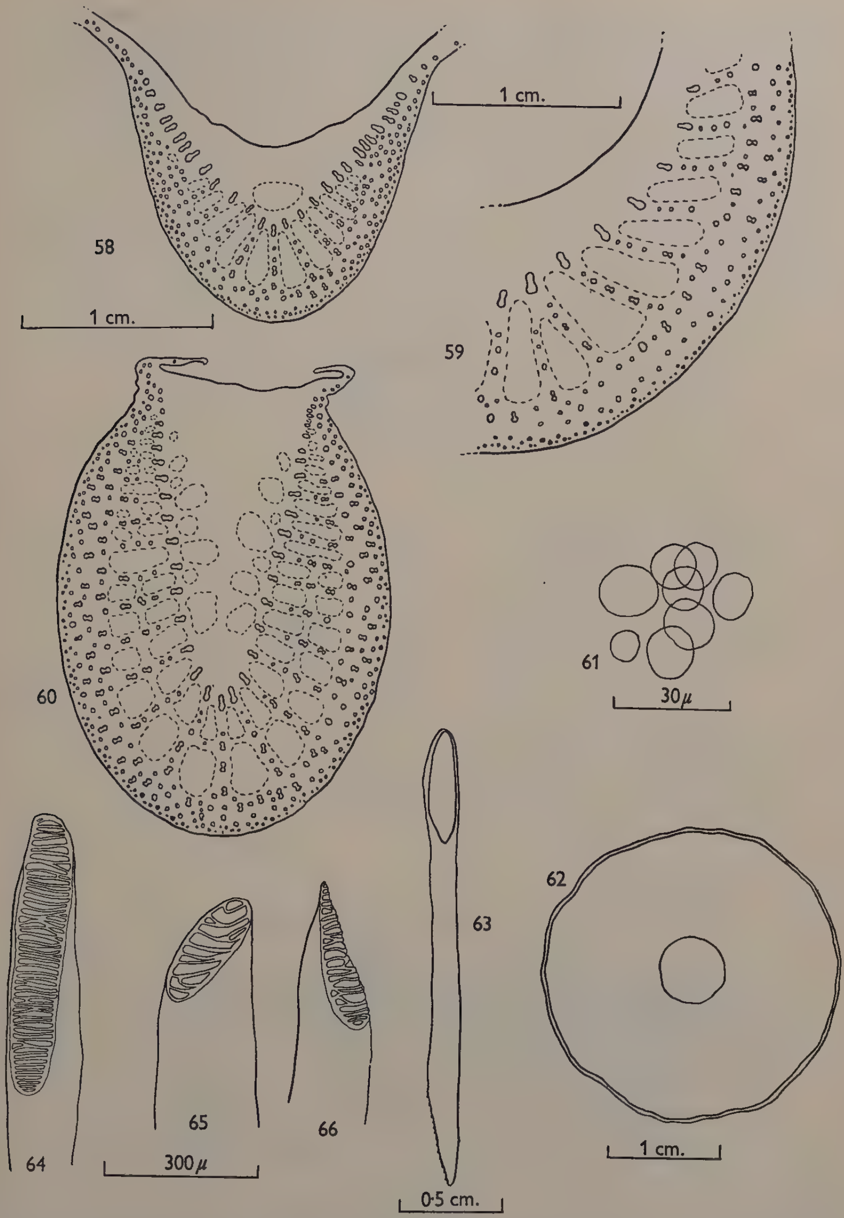
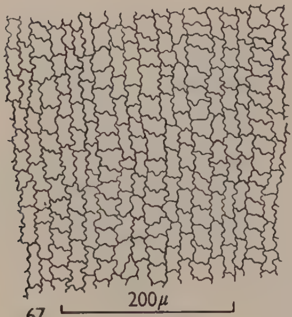


Figs. 48–66. Anatomy of *Strelitzia*. 48. Adaxial epidermis, surface view (*S. reginae*). 49. Abaxial epidermis, surface view (*S. reginae*). 50. T.S. lamina, mechanical tissue (solid black), xylem (lined), phloem (stippled) (*S. reginae*). 51. Silica-cells adjacent to fibre buttress of lamina as seen in T.S. (*S. reginae*). 52. Stoma, surface view, abaxial epidermis (*S. reginae*). 53. T.S. adaxial surface layers with hypodermal silica-bodies (hypodermis 1-layered) (*S. nicolai*, young plant). 54. T.S. stoma, abaxial epidermis (*S. augusta*). 55. Silica-bodies in adaxial hypodermis, surface view of costal region (*S. reginae*). 56. T.S. lamina, including a large vein (*S. reginae*). 57. L.S. lamina, transverse commissure in T.S. (*S. nicolai*, young plant). 58. T.S. midrib halfway between its base and apex (*S. nicolai*). 59. T.S. part of leaf sheath (*S. nicolai*). 60. T.S. petiole just below insertion of lamina (*S. nicolai*). 61. Starch grains from stem of *Strelitzia* sp. 62. Outline T.S. of root (*S. nicolai*). 63. Complete vessel element from stem of *S. nicolai* (details of perforation plates not shown). 64–66. End walls of vessel elements from roots of *S. nicolai* and *S. parvifolia*.



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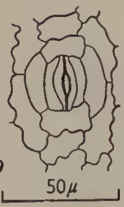

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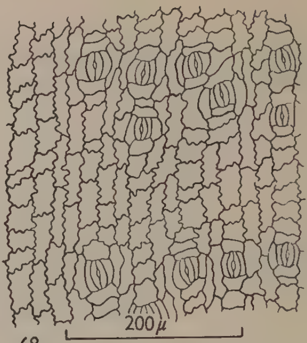

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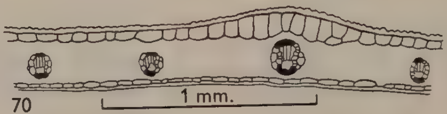

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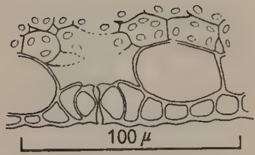

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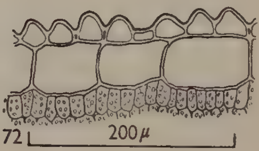

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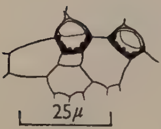

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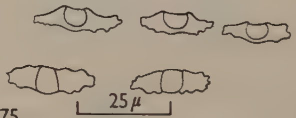

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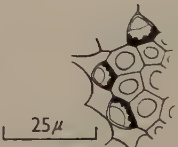

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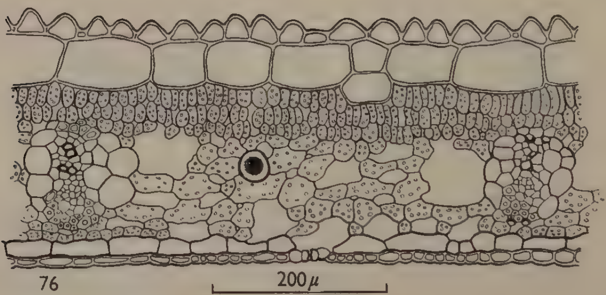

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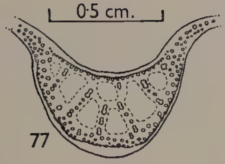
Figs. 67–90. Anatomy of *Heliconia*. 67. Adaxial epidermis, surface view (*H. bihai*). 68. Abaxial epidermis, surface view (*H. bihai*). 69. Stoma, surface view, abaxial epidermis (*H. bihai*). 70. T.S. lamina, mechanical tissue (solid black), xylem (lined), phloem (stippled) (*H. metallica*). 71. T.S. stoma, abaxial surface (*H. spectabilis*). 72. T.S. adaxial surface layers (*H. metallica*). 73. Stegmata adjacent to bundle-sheath parenchyma (from T.S. lamina of *H. metallica*). 74. Stegmata adjacent to bundle-sheath fibres (from T.S. lamina of *H. metallica*). 75. Silica-bodies from lamina (*H. metallica*). 76. T.S. lamina (*H. metallica*). 77. T.S. midrib halfway between its base and apex (*H. bihai*). 78. T.S. petiole, just below insertion of the lamina (*H. bihai*). 79. T.S. middle of petiole (*H. bihai*). 80. T.S. distal part of leaf sheath (*H. bihai*). 81. T.S. leaf sheath (*H. bihai*). 82. Stellate parenchyma of transverse diaphragm in air-canal of petiole (*H. metallica*). 83. Enlargement of an adaxial part of 80, sclerotic hypodermis. 84. Enlargement of an abaxial part of 80, hypodermis and abaxial fibres. 85. Outline T.S. of root (*H. bihai*). 86. T.S. stele of root showing phloem (solid black) and xylem (open circles) (*H. bihai*). 87. Starch grains from rhizome of *H. bihai*. 88–90. End walls of vessel elements (*H. aurantiaca* and *H. psittacorum*).

S. & M. Main lateral **veins** infrequently buttressed to the adaxial hypodermis and always separated from the abaxial hypodermis by assimilating tissue (Fig. 70); other veins not connected to either hypodermis by buttresses. Bundle-sheaths mostly composed of fibres above and below, but smallest bundles sheathed only by parenchyma adaxially; lateral parenchyma of bundle-sheaths often 2-layered. **Transverse commissures**, situated at the same level as the longitudinal veins, and sheathed by parenchyma not forming vertical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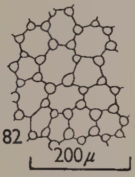
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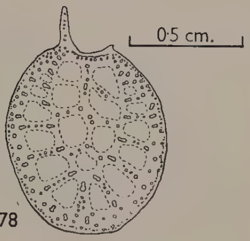
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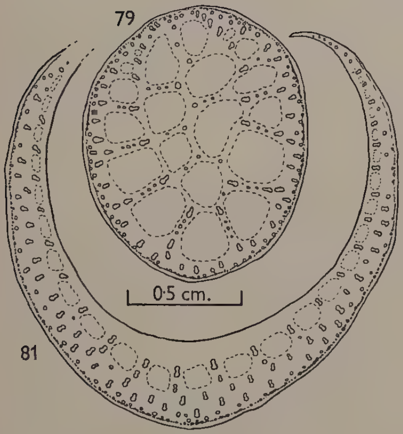
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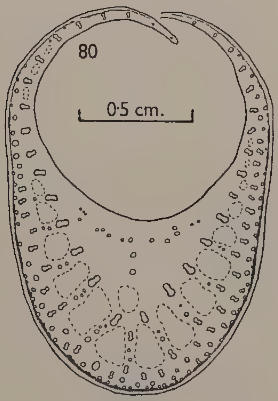
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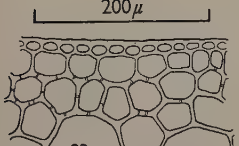
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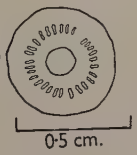
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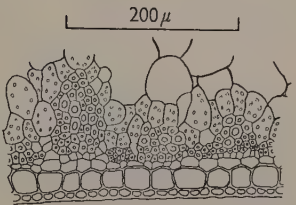
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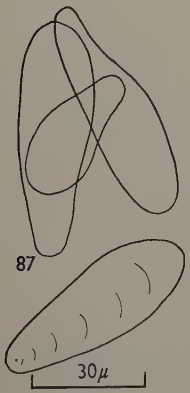
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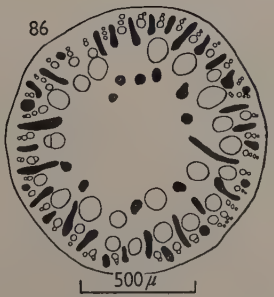
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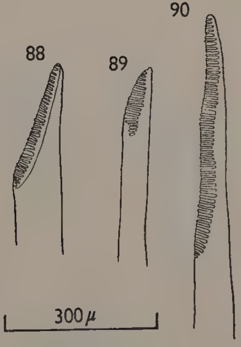
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septa across the mesophyll. **Expansion cells** formed by enlargement of hypodermal cells above the main lateral veins (Fig. 70). 'Pulvinar band', at junction of lamina and midrib, absent.

Midrib, petiole and leaf-sheath (Figs. 77–84)

Epidermis composed of cells with linear walls. **Vascular** and **fibre bundles** present on the adaxial side of the main arc of vascular bundles in the midrib and petiole, and extending to the base of the leaf sheath in certain species, e.g. *H. metallica*. **Air-canals** present at all levels as a single arc on the abaxial side of the vascular bundles, additional canals (unlike *Musa*) being situated on the adaxial side of the vascular bundles in the midrib and petiole. **Transverse diaphragms** (Fig. 82) 1, or more, layered, as in *Musa*. **Chlorenchyma** forming a distinct adaxial band in the midrib and petiole; abaxial chlorenchyma (unlike *Strelitzia* and *Ravenala*) absent. Cells immediately beneath the abaxial epidermis always thin-walled (Fig. 84), never sclerotic as in *Musa, Ravenala* and *Strelitzia*. Other ground tissue somewhat variable, but probably distinctive for each species as shown by the following examples: (i) *Heliconia aurantiaca*, ground parenchyma not sclerotic, abaxial fibre bundles absent from the petiole. (ii) *H. bihai*, adaxial hypodermis somewhat sclerotic in upper part of leaf sheath (Fig. 83); abaxial fibres fused into a ± continuous layer at all levels; hypodermal cells, and sometimes the epidermal cells adjacent to abaxial stomata, sclerosed. (iii) *H. psittacorum*, abaxial ground parenchyma never sclerotic, but sclerosis sometimes associated with stomata; adaxial hypodermis sclerotic in petiole; abaxial fibres fused into a continuous layer in midrib and petiole. (iii) *H. spectabilis*, ground parenchyma not sclerosed; abaxial fibre strands always discrete, never in a continuous layer.

Rhizome

Short or creeping, fibrous. **Periderm** divisions absent, or occasional in old rhizomes. **Vascular bundles** very tortuous; those in the cortex with well-developed fibre sheaths adjacent to the phloem; those of the central cylinder either without fibrous sheaths or with narrow, continuous sheaths of fibres; central bundles often amphivasal. Fibre bundles common in the cortex. Cortical ground parenchyma somewhat aerenchymatous in *H. psittacorum*.

Root (Figs. 85, 86)

Periderm divisions absent. **Exodermis** of thin-walled, suberized cells. Inner cortex containing radial **air-canals** (Fig. 85). Pericycle 1-layered. **Stele** with normal structure but phloem groups often radially extended towards the centre of the stele and sometimes cut off as isolated strands internal to the metaxylem strands (e.g. *H. bihai* (Fig. 86)).

Stegmata, crystals, tannin, starch and laticifers

Stegmata in longitudinal files adjacent to the fibres (occasionally parenchyma) of the bundle-sheaths, the cell walls adjacent to the fibres being slightly thickened and pitted (Fig. 74), each cell containing a rectangular, 'trough-shaped' (S. & M.) silica-body, with a central depression, much deeper than the depressions in the silica-body of *Musa*, and dividing each body almost into two (Fig. 75). Silica-bodies spinous, the spines said to penetrate pits in the walls of the silica-cells. Stegmata abundant in aerial parts of the plant and beside the leaf traces in the rhizome. (ii) Vascular bundles of rhizome, especially those of the central cylinder, often accompanied by files of small thin-walled cells (particularly conspicuous in young rhizomes), each cell containing an irregular or spherical, smooth or granulose silica-body. Silica-cells not accompanying the transverse veins of the lamina, as in *Musa, Ravenala*, and *Strelitzia*; silica absent from the root.

Crystals present in all parts; scattered; sometimes in the form of crystal-sand, e.g. in the lamina and rhizome; raphide sacs common. **Starch** (Fig. 87) present as cylindrical-ellipsoidal, not flattened grains; most abundant in storage rhizomes. **Tannin** common in all parts in morphologically unspecialized cells. **Laticifers** absent.

Vessels (Figs. 88–90)

True vessels confined to the metaxylem of the root; constituent elements 35–150μ in diameter and 840–3170μ long, with long scalariform perforation plates in very oblique end walls.

(6) Orchidantha

Lamina

Main lateral veins arising at an acute angle to midrib, ± parallel with midrib. Leaf dorsiventral. **Hairs** absent. **Cuticle** thin; epidermis never wholly cutinized. **Epidermis**; adaxial epidermis (Fig. 91) uniform, with the cells in distinct, fairly regular, long or short files, the files being parallel to the main lateral veins; cells rectangular or isodiametric in surface view, but shape rather variable; walls linear or somewhat curved. Abaxial epidermis (Fig. 92) not differentiated into costal and intercostal regions; cells in distinct files and similar in shape and size to those of the adaxial epidermis. Cells of each epidermis in transverse section appearing to be approximately uniform in size, flattened, especially those of the adaxial surface (Fig. 94); walls not thickened. **Stomata** infrequent on the adaxial surface, those on the abaxial surface ± uniformly scattered but sparse; not in distinct files; 31·5–55·5μ long, guard cells not sunken and, unlike those of other genera, with prominent median wall thickenings (Fig. 96). Terminal subsidiary cells scarcely differentiated from other epidermal cells, other cells adjacent to stomata not specialized (Fig. 95). Cell files adjacent to stomata not displaced. **Hypodermis** 1-layered beneath each surface, but not well differentiated from the assimilating mesophyll (Figs. 93, 97). Adaxial hypodermal cells in uniform longitudinal files, the individual cells being transversely extended; abaxial hypodermis similar, but cells smaller and more nearly cubical; four hypodermal cells usually adjacent to each substomatal chamber, and occasionally containing chloroplasts. Independent fibres or fibre bundles present in all species (few in *Orchidantha calcarea*), either adjacent to each hypodermis, or separated from each hypodermis by a single file of assimilating cells (Figs. 93, 94); fibres occasionally adjacent to the epidermis. **Mesophyll**; palisade tissue not differentiated, the chlorenchyma consisting of an irregular mixture of large and small cells (Figs. 97, 99). Large cells often appearing colourless in sections, but containing as many chloroplasts as the small cells. Longitudinal **veins** remote from each other; situated adaxially, and always separated from the abaxial surface by several mesophyll layers (Fig. 93). Adaxial fibres of the bundle-sheaths usually in contact with the hypodermis. Parenchyma of bundle-sheaths always 1-layered. **Transverse vascular bundles** situated abaxially, often running beneath the longitudinal veins without making contact with them; large, conspicuous to the naked eye; cylindrical and each with a well-developed sheath of thick-walled cells (Fig. 98). **Expansion cells** and 'pulvinar band' absent.

Midrib, petiole, leaf sheath (Figs. 102–105)

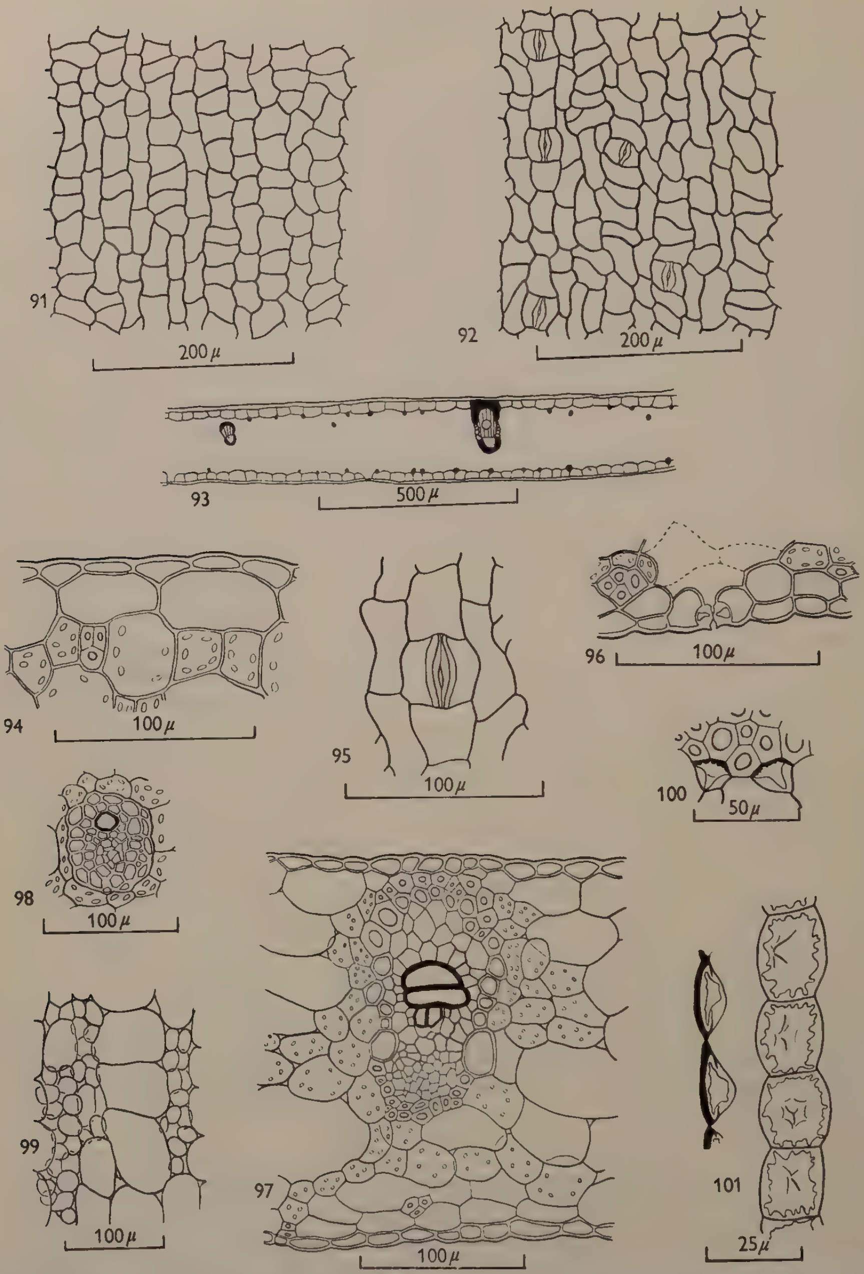
Midrib, petiole and leaf sheath gradually confluent and not sharply delimited from each other, as in other genera. Adaxial fibre and vascular bundles well developed in the leaf sheath and present at all levels. Rather narrow **air-canals** present in two distinct abaxial arcs throughout the greater part of leaf stalk; adaxial air-canals occur in the upper part of the sheath, petiole and proximal part of midrib. Chloroplasts diffuse, not limited to any part of the leaf stalk. **Hypodermis** never sclerotic or differentiated from the rest of the ground tissue. **Diaphragms** 1, or more, layered; stellate cells not as long-armed as in other genera, the air-canal being narrow.

Rhizome

Short, narrow, erect. **Periderm** well developed in old rhizomes, arising by division of cells in the outer cortex. Fibre bundles occasional in outer cortex except in *O. maxillarioides*. **Endodermis** and vascular complex well developed. Cortical bundles, accompanied by well-developed fibre sheaths, around the phloem, but leaf traces gradually losing their fibre sheaths on entering the central cylinder. Vascular tissues of the central bundles irregularly arranged, the xylem often surrounding the phloem.

Root

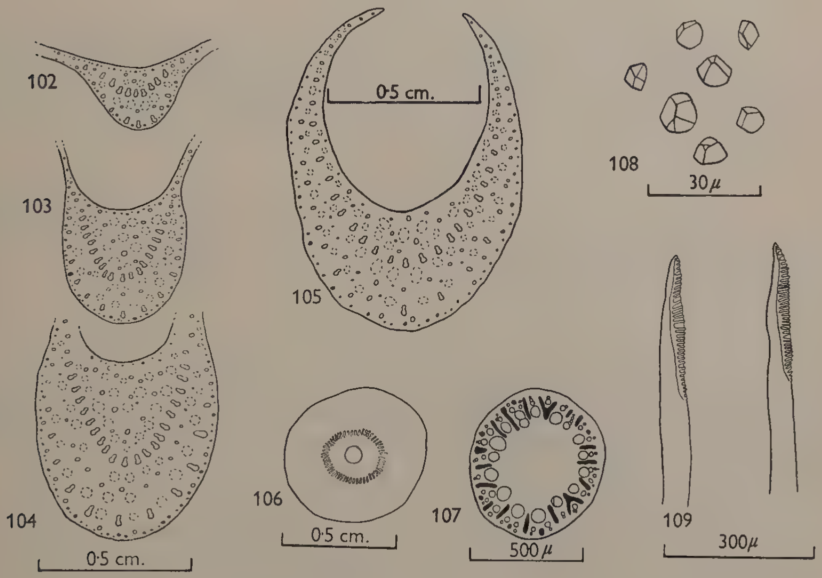
Roots sometimes with localized swellings consisting of an enlarged cortex. **Periderm** divisions absent; exodermis of thin-walled, ligno-suberized cells always conspicuous in mature rhizomes. **Air-canals** present in the inner cortex (Fig. 106); sometimes small. **Stelar structure** normal (Fig. 107), but phloem groups centripetally extended, and very occasionally isolated as central strands (*O. longiflora*).



Figs. 91–109. The anatomy of *Orchidantha* (*O. longiflora*). 91. Adaxial epidermis, surface view. 92. Abaxial epidermis, surface view. 93. T.S. lamina, mechanical tissue (solid black), xylem (lined), phloem (stippled). 94. T.S. adaxial surface layers. 95. Stoma, surface view, abaxial epidermis. 96. T.S. stoma, abaxial surface. 97. T.S. of a main vein of the lamina. 98. T.S. transverse commissure. 99. Mesophyll of lamina in paradermal view. 100. Stegmata adjacent to bundle-sheath fibres of a vascular bundle in the petiole. 101. Stegmata of lamina in surface and lateral view. 102. T.S. midrib halfway between its apex and base. 103. T.S. transition region between midrib and petiole. 104. T.S. distal part of leaf sheath. 105. T.S. leaf sheath. 106. Outline T.S. of root. 107. T.S. stele of root showing distribution of phloem (solid black) and xylem (open circles). 108. Starch grains from rhizome. 109. End walls of vessel elements from the root.

Stegmata, silica-bodies, crystals, tannin, starch and laticifers

Stegmata (Figs. 100, 101) forming longitudinal files adjacent to the fibres in all organs except the root; silica-bodies 'hat-shaped' (S. & M.), with basal projections said to penetrate pits in the thicker-walled part of the silica-cells adjacent to the fibres. Large, but rather irregular silica-bodies abundant in the rhizome, the files of cells containing them forming almost complete investments to the mechanical part of the sheaths of the leaf traces in the cortex and central cylinder. **Crystals** of calcium oxalate common in all parts; crystal-sand abundant in rhizomes; raphide sacs common, especially in the rhizome. **Tannin** absent from the transverse diaphragms of the air-canals in the leaf stalk (unlike other genera); most abundant in the rhizome and absent from the root. **Starch** (Fig. 108) as small, angular, more or less isodiametric, unflattened grains; abundant in the rhizome and also common in the petiole. **Laticifers** absent.



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Vessels (Fig. 109)

True vessels confined to the metaxylem of the root; elements 24–43 μ in diameter and 935–2930 μ long, resembling tracheids but with scalariform perforation plates in the long, very oblique end walls. Vessels not recorded in the root by S. & M.

APPENDIX B

MATERIAL EXAMINED

Musa

M. basjoo Siebold. (lamina, Kew); *M. malaccensis* Ridl. (leaf, Botanic Gardens, Singapore); *M.* '*paradisiaca*' (W. African plantain, all parts, Kibi, Gold Coast); *M.* '*sapientum*' (edible banana, lamina, Kew; all parts, Botany Department, University of Malaya; all parts, Botanic Gardens, University College of the Gold Coast); *M. sumatrana* Becc. (leaf, Botanic Gardens, Singapore); *M. textilis* Nee. (leaf, Botany Department, University of Malaya); *M. violascens* Ridl. (leaf, Botany Department, University of Malaya).

Ensete

E. arnoldianum (De Willd.) Cheesm. (leaf and root, Aburi, Ghana); *E. gilletii* (De Willd.) Cheesm. (leaf and root, Bamenda, British Cameroons); *E. ventricosum* (Welw.) Cheesm. (leaf, Kew).

Ravenala

R. madagascariensis Gmel. (all parts, Botanic Gardens, Singapore; leaf, Kew; leaf, Botanic Gardens, University College of the Gold Coast).

Strelitzia

S. augusta Thunb. (leaf and root, Kew); *S. nicolai* Regel & Koch (all parts, Kew; young plant, leaf, Botanic Gardens, Singapore); *S. parvifolia* Dryand. (leaf and root, Kew); *S. reginae* Banks. (leaf and root, Botanic Gardens, University College of the Gold Coast; rhizome, Kew); *Strelitzia* sp. (stem, Rhodesia).

Heliconia

H. aurantiaca Chiesb. (all parts, Botanic Gardens, Singapore); *H. bihai* Linn. (all parts, Botanic Gardens, Singapore); *H. metallica* Planch. & Lind. (all parts, Botanic Gardens, Singapore); *H. psittacorum* Sesse & Moe. (all parts, Singapore); *H. rostrata* Ruis. & Pav. (leaf, Kew); *H. spectabilis* Lindl. & Rodigas. (all parts, Botanic Gardens, Singapore).

Orchidantha

O. calcarea Henders. (leaf, Botanic Gardens, Singapore); *O. longiflora* Ridl. (all parts, Botanic Gardens, Singapore); *O. maxillarioides* K.Schum. (all parts, Botanic Gardens, Singapore); '*Lowia meleagris*' (all parts, Kew).

SUMMARY

The morphology and existing schemes of classification of the genera of Musaceae have been summarized. The anatomy of the vegetative organs of each genus has been described. The following taxonomic conclusions are suggested by the anatomical results:

(i) *Orchidantha* is anatomically quite distinct from other members of the group and its isolation as a distinct family (Lowiaceae) is fully supported.

(ii) *Ravenala* and *Strelitzia* are almost identical anatomically and are evidently much more closely related to each other than they are to any other genera.

(iii) *Musa* is quite distinct anatomically, although it shows some affinities with the *Ravenala–Strelitzia* complex.

(iv) *Heliconia* is also rather isolated structurally, but shows more affinities with *Ravenala*, *Strelitzia* and *Musa* than with *Orchidantha*.

ACKNOWLEDGEMENTS

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I should also like to thank the following:

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A contribution to the life history of Synedrella nodiflora Gaertn.

By I. Banerji, F.L.S. and Sunanda Pal, Department of Botany,
Calcutta University, India

(With 51 Text-figures)

[Read 21 November 1957]

Although the cytology and embryology of the various members of the Compositae have been studied both in India and elsewhere in recent years, no reference to the genus *Synedrella* has been noted. The present investigation of the annual monsoon weed *S. nodiflora* was undertaken with a view to filling this gap. The earlier literature on the family has been reviewed by Schnarf (1931), and the later work by Banerji (1940, 1942), Maheshwari (1950), and Venkateswarlu & Maheshwari Devi (1955*a*, *b*) and hence it need not be repeated here.

Material and methods

The material with the involucral bracts removed was fixed in weak formalin–acetic–alcohol and Nawaschin's fluid between 10 a.m. and 12 noon. Sections, 8–14μ thick, were stained with Heidenhain's and Delafield's haematoxylin for embryological studies, while Newton's Crystal violet-iodine was used for cytological investigations. The morphology of the somatic chromosomes was studied from smear preparations of the root-tips, which were pretreated for an hour at 14–16° C. in 0·005 % aqueous solution of Coumarin. They were then fixed in acetic–alcohol (1:2) for half an hour, and subsequently hydrolysed in normal HCl at 60° C. for 12 min., followed by heating in 2 % aceto-orcein for 3–5 min. at 60° C. and finally squashed in 1 % aceto-orcein.

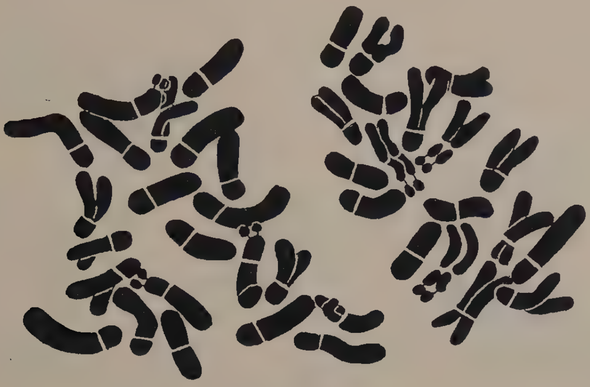
Observations

Somatic chromosomes. The somatic number of chromosomes was found to be 40 (Fig. 1). An analysis of the karyotype reveals that the chromosomes are small, varying in length between 4·04 and 2·35μ. The idiogrammatic representation of the chromosomes shows thirteen types which can be classified into three categories on the basis of their relative lengths (Fig. 2). (1) Three pairs of long chromosomes, two pairs with subterminal centromere, while the third pair has a submedian centromere and satellite on the shorter arm. (2) Thirteen pairs of medium-sized chromosomes: three pairs with subterminal, five pairs with submedian and three pairs with nearly median centromeres, while of the other two pairs each has a submedian centromere and satellite on the shorter arm. (3) Four pairs of short chromosomes: two pairs with subterminal and the other two pairs with submedian centromeres. It should be stated here that pairs of chromosomes with more or less identical morphology but with slight variation in length have been placed under the same type.

Organogeny. In the development of a disk floret, the petals first arise as papillate outgrowths, the tips of which soon curve inwards. The primordia of the stamens arise on the inner side of the petals and soon become differentiated into comparatively long anthers and short filaments. The sepals next differentiate as spinous processes. The primordia of the two carpels arise on the inner side of the stamen and close to the centre of the floral axis. In the early stages of their development they lie side by side, but later their distal ends meet and form the solid style, while the proximal end separates out to form the ovarian chamber. The carpels open out again at the apex to form the bifid stigma clothed with unicellular hairs.

Microsporogenesis. In the mature anther the two-layered sporogenous cells are separated from the epidermis by three layers of cells, of which the innermost layer forms the tapetum (Fig. 3). Both the parietal layers persist in the mature anther.

The early stages of meiosis have not been studied. At diakinesis 20 bivalent chromosomes are noted, of which three are seen to be attached to the nucleolus (Fig. 4). The chromosomes undergo condensation and appear as spherical bodies. The nucleolus and the nuclear membrane gradually disappear and the gemini move towards the centre of the nucleus. At metaphase I, secondary association of bivalents is noted (Figs. 5–9).



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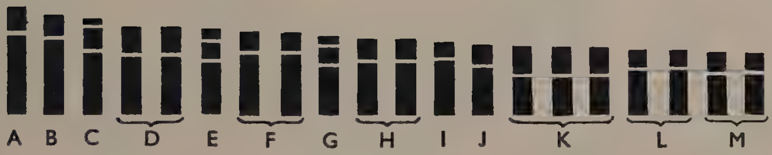

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Fig. 1. Somatic metaphase plate showing 40 chromosomes, × 3400.

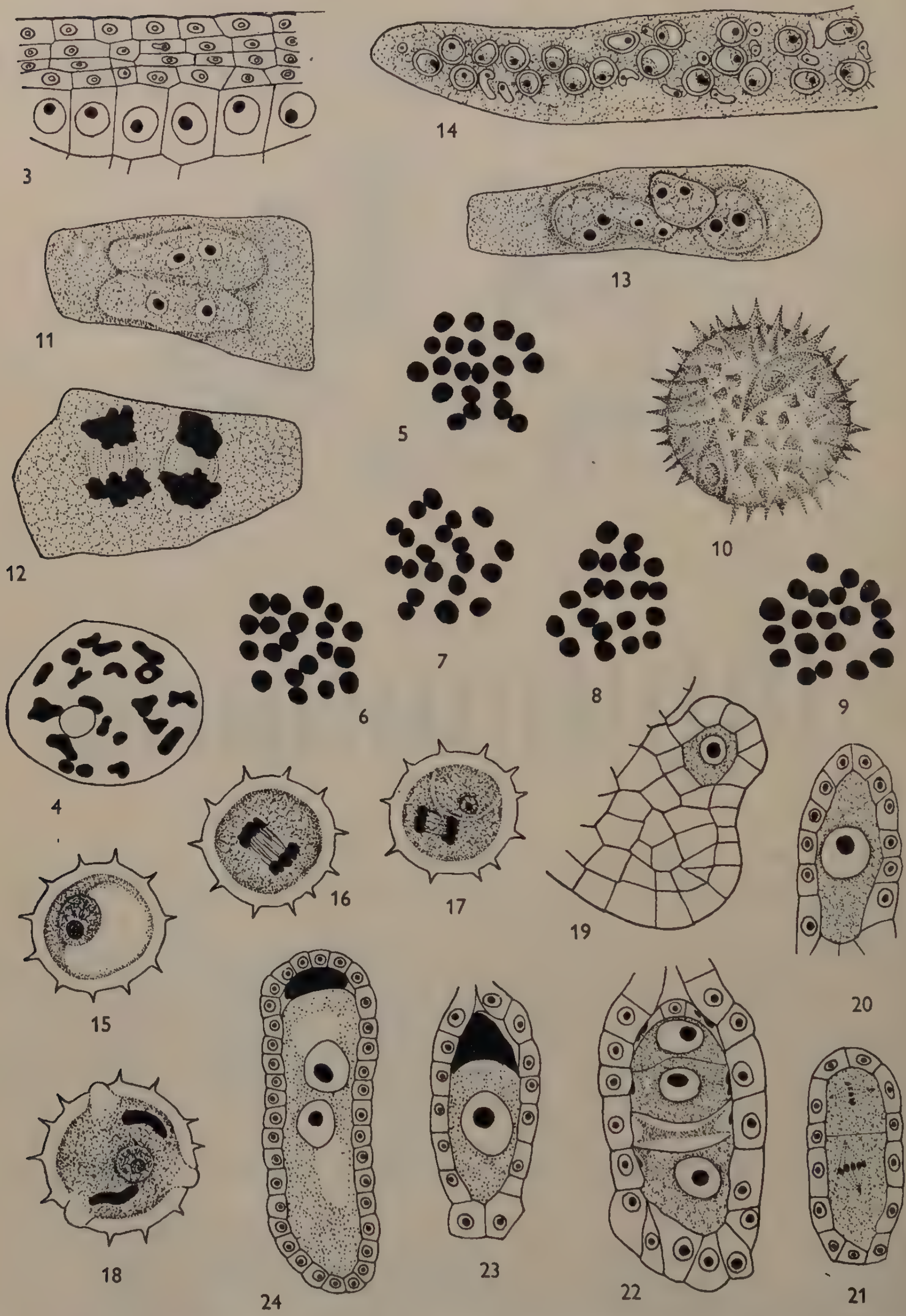
Fig. 2. Idiogrammatic representation of the somatic complement of chromosomes, × 3400.

An analysis of the different types of association is presented in Table 1.

The maximum association of bivalents, as will be evident from Table 1, has been found to be 7 (2) + 6 (1), suggesting that the basic number is 13.

Table 1. *Different types of association of bivalents and their frequencies*

Configurations	Units of grouping	Maximum association encountered	No. of times observed out of 100 clear plates
1. 2 (2) + 16 (1)	18	—	12
2. 1 (3) + 1 (2) + 15 (1)	17	—	6
3. 1 (3) + 2 (2) + 13 (1)	16	—	12
4. 2 (3) + 1 (2) + 12 (1)	15	—	8
5. 2 (3) + 2 (2) + 10 (1)	14	—	12
6. 1 (4) + 1 (3) + 1 (2) + 11 (1)	14	—	8
7. 1 (3) + 4 (2) + 9 (1)	14	—	24
8. 2 (3) + 3 (2) + 8 (1)	13	—	10
9. 7 (2) + 6 (1)	13	13	8



Figs. 3–24. Fig. 3. Differentiation of the sporogenous cells in the anther, × 525. Fig. 4. Diakinesis showing 20 bivalents, × 1700. Figs. 5–9. Different types of secondary association in metaphase I, × 1700. Fig. 10. Pollen grain, × 715. Figs. 11–13. Figures illustrating the nuclear condition in the tapetal cells, × 1100. Fig. 14. Part of an anther lobe (*l.s.*) showing tapetal periplasmodium surrounding the pollen-grains, × 148. Figs. 15–18. Various stages of the development of male gametophyte, × 715. Figs. 19, 20. Differentiation of the megaspore-mother cell, × 440. Fig. 21. Formation of the T-shaped tetrad, × 440. Fig. 22. Linear tetrad of megaspores, × 525. Fig. 23. Functioning chalazal megaspore, × 440. Fig. 24. 2-Nucleate embryo-sac, × 525.

Side views of metaphase I show that the bivalents are regularly aligned on the equatorial plate, and the movement of the univalents at anaphase I is regular. On reaching the poles the chromosomes organize interkinetic nuclei, and then undergo the second division which is also quite regular. The microspores show mostly a tetrahedral arrangement. Cytokinesis takes place by the process of furrowing.

The pollen grains when liberated from the microsporangium are ellipsoidal in outline, but become spherical in contact with moisture. They are trinucleate, have an average diameter of 20μ, and are echinate. Four short spindle-shaped furrows are present, in the centre of each of which a germ pore is situated. In most cases the intine protrudes through it as a tiny papilla (Figs. 10, 18).

The tapetal cells of the anther are densely protoplasmic and become binucleate during synizesis of the pollen mother cells (Fig. 11). Normally this binucleate condition persists till the end of the second division of the pollen mother cells; afterwards one or both of the nuclei of the tapetal cells divide once again resulting in the trinucleate or tetranucleate condition (Figs. 12, 13). Along with the differentiation of the exine of the microspores, the radial walls of the tapetal cells become indistinct. Gradually the cells form a plasmodium and fill up the inside of the microsporangium completely (Fig. 14). The microspores lie embedded in the tapetal plasmodium, the nuclei of which appear to be somewhat elongated and lie in groups.

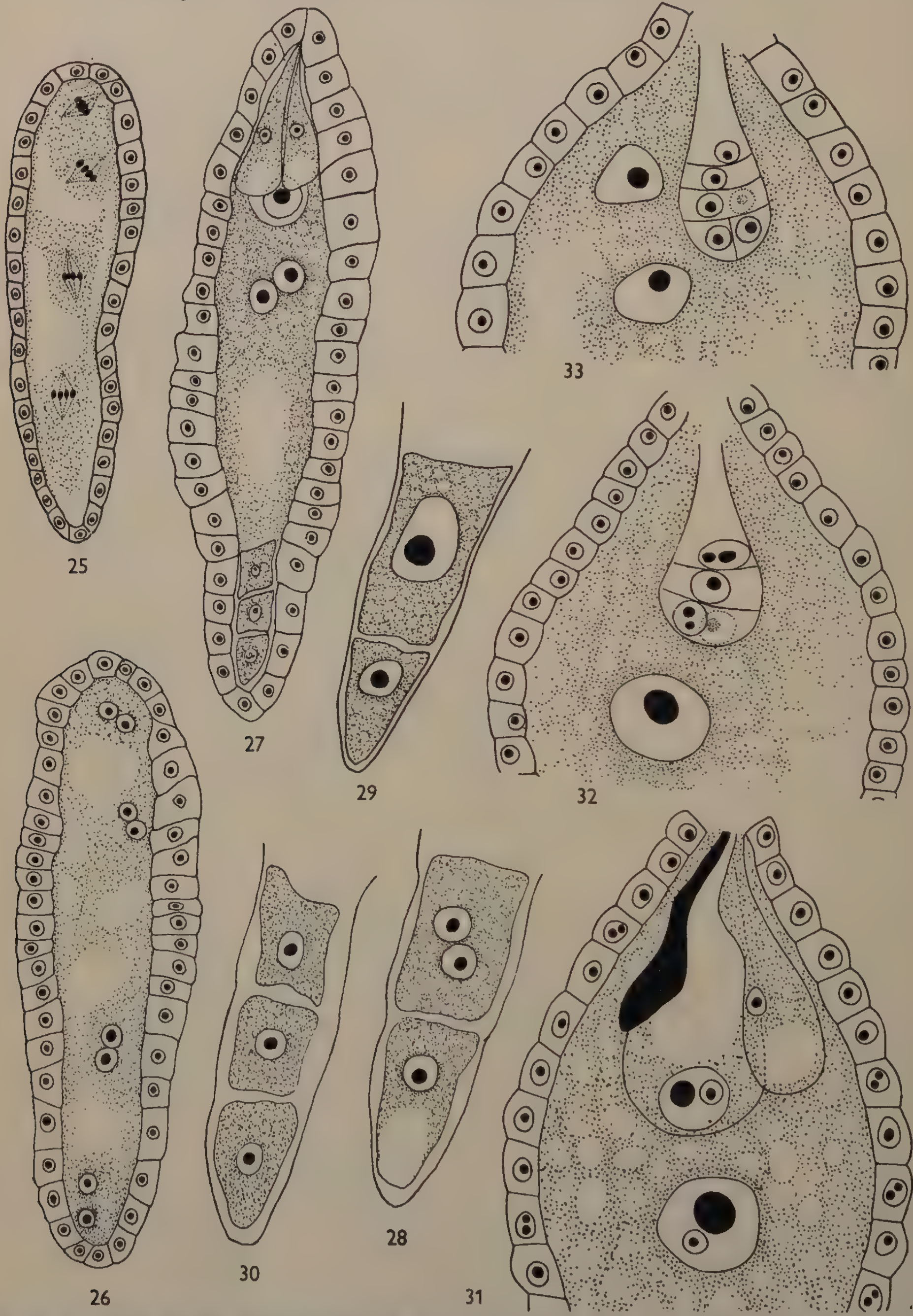
Male gametophyte. The nucleus of the microspore divides while inside the microsporangium, and of the two nuclei thus produced the smaller one becomes separated by a cytoplasmic membrane. Later, they lie in a common mass of cytoplasm. The generative nucleus soon divides to produce two sperm nuclei which are rod-shaped in appearance. The various stages of the development of the male gametophyte are illustrated in Figs. 15–18.

Megasporogenesis and female gametophyte. The archesporial cell is hypodermal and develops directly into the megaspore-mother cell (Figs. 19, 20). It undergoes reduction division and produces a linear tetrad of megaspores. Only in one instance was a T-shaped tetrad observed. The chalazal megaspore always becomes functional (Fig. 23). The disintegration of the other megaspores takes place from below upwards (Fig. 22). As the functioning megaspore increases in size, the single layer of nucellar cells encasing it degenerates and the embryo-sac lies in close contact with the inner layer of cells of the integument which differentiates into the integumentary tapetum. The nucleus of the functioning megaspore divides thrice in succession to produce a ‘Polygonum type’ of embryo-sac.

In the fully differentiated embryo-sac the synergids are pear-shaped structures with long pointed ends. The egg cell is larger than the synergids. The two polar nuclei fuse early and the secondary nucleus lies close to the egg. There are generally two antipodal cells, of which the upper is binucleate (Fig. 28). The nuclei often fuse together to produce a diploid nucleus which is larger in size (Fig. 29). In a few instances, however, three uninucleate antipodal cells arranged in a linear order have also been observed (Fig. 30). The antipodals persist for a long time and have been found in the embryo-sac even in advanced stages of the development of the embryo.

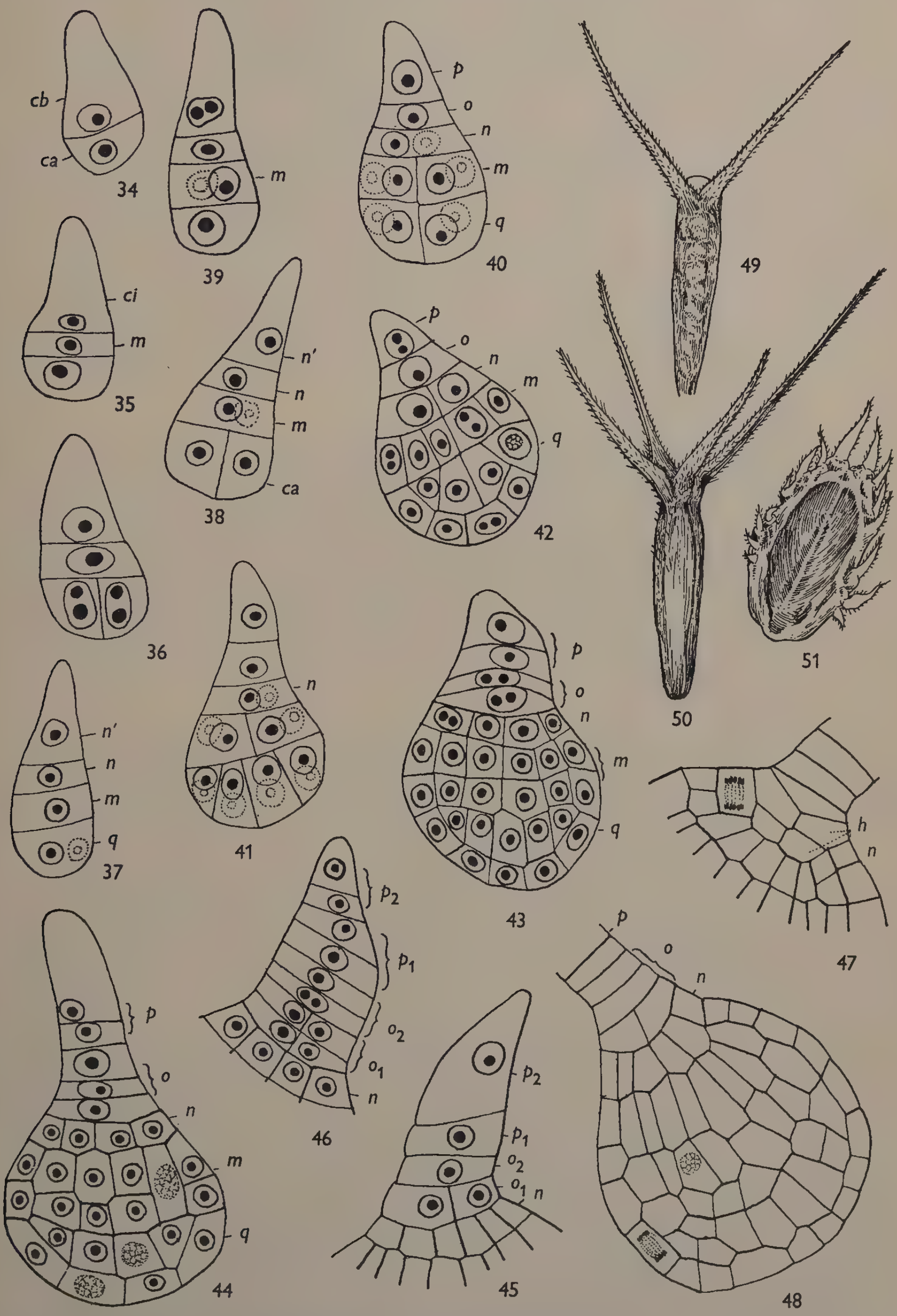
Fertilization. The pollen tube enters the ovule by way of the micropyle and discharges the two sperm nuclei inside the embryo-sac. One of the synergids is destroyed in this process and the other degenerates after fertilization. Triple fusion and syngamy take place more or less simultaneously (Fig. 31). The sperm nuclei appear spherical at this stage. The embryo-sac increases in size after fertilization and contains the oospore, the primary endosperm nucleus and the antipodals.

Endosperm. The primary endosperm nucleus divides before the fertilized egg. The division is not accompanied by the formation of a cell wall. In most cases, wall formation takes place at the eight-nucleate stage of the endosperm. In a few cases, the development of the endosperm is very belated. In one embryo-sac, a four-celled proembryo was found in association with an undivided primary endosperm nucleus. In another embryo-sac the proembryo was six-celled, while the endosperm was only two-nucleate (Figs. 32, 33). In the mature seed the endosperm is nearly absent and only a thin lining layer surrounds the embryo.



Figs. 25–33. Figs. 25–27. Development of the embryo-sac. Fig. 25, × 282. Figs. 26, 27, × 440. Figs. 28, 29. Two-celled antipodal, × 440. Fig. 30. Three uninucleate antipodal cells, × 440. Fig. 31. Double fertilization, × 525. Figs. 32, 33. Cases of delayed development of the endosperm, × 440.

Embryo. The fertilized egg divides transversely to give rise to *ca* and *cb* (Fig. 34). The basal cell again divides transversely, forming *m* and *ci* (Fig. 35). Next, *ca* divides longitudinally either prior to, or simultaneously with the transverse division of *ci* into *n* and *n′* (Figs. 36, 37). This is followed by vertical division of *m* (Fig. 38). In one instance, how-



Figs. 34–51. Stages of the development of the embryo. Figs. 34, 35, × 283. Figs. 36–48, × 440. Figs. 49–51. Structure of the fruit, × 5.

ever, the first vertical division appeared in *m* of the linear four-celled proembryo (Fig. 39). Next, the cells *ca* and *m* divide vertically at right angles to the previous plane of division to give rise to two tiers of juxtaposed cells producing the octant stage (Fig. 40). Meanwhile, the cell *n* divides vertically and *n′* undergoes division forming *o* and *p* (Fig. 42). The cells of the apical quadrant *q* divides in an obliquely vertical plane to produce eight cells in one tier (Fig. 41). Periclinal divisions next take place in the cells of the tiers *q* and *m* which also extends to *n*, resulting in the differentiation of a single layer of dermatogen (Figs. 42, 43). The other two histogenic layers are derived by the anticlinal and periclinal divisions of the cells bounded by the dermatogen.

The basal cells *o* and *p* divide transversely to give rise to o_1 and o_2 and p_1 and p_2 (Figs. 43, 45). The next division of o_1 is generally vertical, but in some cases it may be transverse (Figs. 44, 45), where both the resultant cells divide vertically (Fig. 46). In several instances more transverse divisions are noted in the suspensor cells (Fig. 46). Meanwhile, transverse divisions occur in the cell derivatives of *m* and thus it becomes two-tiered.

The cells of the tier *q* ultimately give rise to the stem-tip and the two cotyledons. The cells of the next tier *m* produce the hypocotyl. The derivatives of *n* give rise to the initials of the central cylinder of the root and to the lateral portions of root-cap. The development of the hypophysial cell o_1 is rather belated; it forms the initials of the root-cortex and the median portion of the root-cap (Figs. 47, 48).

Structure of the fruit. The ray florets and disk florets both mature into fruits which vary in size and shape. The fruits developing from the disk florets are elongated and tubular with two to four long, hard processes at the top derived from the persistent sepals. The processes are covered by numerous thin and short hair-like outgrowths (Figs. 49, 50). On the other hand, the ray florets develop into flat, broad and slightly elongated fruits possessing numerous hairy outgrowths on the margin, projecting outwards and upwards (Fig. 51). These fruits are more massive than those developing from the disk florets.

The seeds of both types of fruit show the presence of well-developed embryos and are viable.

DISCUSSION

Synedrella nodiflora belongs to the tribe Heliantheae of the family Compositae. Cytological investigations on various members of the family have been carried out by Lawrence (1931), Cooper & Mahony (1935), Babcock (1947), Clausen (1951), and others. It is interesting to note that secondary association of chromosomes was observed in *Dahlia* as early as 1929 by Lawrence. Since then it has been recorded in a number of plants by different workers. The maximum association in *Synedrella nodiflora* appears to be 7 (2) + 6 (1) which indicates that the basic number of chromosomes is 13. Assuming the theory of secondary association to be correct, the present observations lead to the conclusion that *S. nodiflora* is a secondary balanced polyploid derived from the basic number 13.

The somatic chromosome number of *S. nodiflora* is 40, which appears to be the first record in this genus. This number has not yet been recorded in the tribe Heliantheae though higher numbers have been observed in a few genera, such as *Bidens*, *Helianthus*, etc. (Darlington & Wylie, 1955). The chromosome number $2n = 40$, however, is recorded in several genera belonging to other tribes of the family.

In *Synedrella nodiflora* the tapetal plasmodium is late in development. It is preceded by nuclear divisions in the tapetal cells which in this plant become quadrinucleate. Bhargava (1935) reports four to five nuclei in a single cell of *Eclipta erecta* L. Mitra (1947) also records the presence of four nuclei in the tapetal cells of *Ageratum conyzoides* L., *Mikania scandens* Willd., *Grangea maderaspatana* Poir. and *Enhydra fluctuans* Lour.

The morphology of the pollen grains of only a few plants belonging to the tribe Heliantheae has so far been studied. They vary from a tetra to a hexacolporate condition.

As observed in *Tridax procumbens* (Banerji, 1940) the pollen grains of *Synedrella nodiflora* are also tetracolporate, the germ pores being situated in the centre of the furrows. All the genera are characterized by an echinate condition. The size of the pollen grains in species belonging to the tribe Heliantheae vary from 18·0 to 36·8μ. It is interesting to note that the pollen grains of *S. nodiflora* come within the range.

Variations have been recorded by previous workers like Banerji (1940, 1942), Mitra (1947), and others, regarding the condition of the antipodal cells. In *Synedrella*, the number of antipodal cells was almost always two, and three antipodal cells were found only in a very few cases. In the former case the upper cell is generally binucleate, while in the latter all the cells are uninucleate.

Schnarf (1931) records the presence of both nuclear and cellular endosperm in the tribe Heliantheae. In the present material, the endosperm is of the nuclear type but becomes cellular at a very early stage.

The mode of development of the embryo in the present material is somewhat different from that of *Senecio* (Johansen, 1950), and *Tagetes patula* L. (Venkateswarlu & Maheshwari Devi, 1955*b*). The differences relate to the development of the hypophysis and the suspensor. In this case, the suspensor becomes long by transverse divisions as was observed in *Launaea pinnatifida* Cass. (Venkateswarlu & Maheshwari Devi, 1955*a*).

SUMMARY

The somatic chromosome complement in *Synedrella nodiflora* was found to be 40, of which three pairs are satellited. The karyotypes have been analysed. The presence of 20 chromosomes was noted in diakinesis and metaphase I. Secondary association has been noted. The tapetal cells are quadrinucleate and a periplasmodium is formed.

The pollen grains are trinucleate, echinate, ellipsoidal and tetracolporate. The sperm cells are elongated and rod-shaped.

The development of the female gametophyte is of the 'Polygonum type'. The antipodals are generally two in number, the upper cell being binucleate. In rare cases three uninucleate antipodal cells have also been observed. Endosperm formation is of the nuclear type. The embryo development conforms to the *Asterad* type and agrees more or less with the *Senecio variation* of Johansen.

The fruits derived from the disk florets are tubular and have two to three long pointed processes, while those from the ray florets are broad with numerous hairy outgrowths. Both types are viable.

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A revision of the African species of Terminalia. By MAUREEN E. GRIFFITHS†

(Communicated by F. White, F.L.S.)

(With 29 Text-figures)

[Read 24 May, 1957]

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This revision is based on a thesis submitted for the research degree of B.Sc. of Oxford University. The author wishes to express her gratitude to Prof. Sir Harry Champion for allowing part of her time during a period of three years to be spent on this work and for providing many other facilities; to Mr F. White, her supervisor, for encouragement and guidance and for considerable assistance in preparing the present account for publication, and to her examiners, Mr J. P. M. Brenan and Dr L. Chalk, who suggested that her thesis should be published and who made a number of helpful suggestions and corrections to the original text. It is with pleasure that she acknowledges her debt of gratitude to the Directors and Curators of the herbaria from which material has been obtained on loan. Thanks are especially due to the Director, Royal Botanic Gardens, Kew, and the Keeper, Department of Botany, British Museum (Natural History), for allowing part of this work to be done in the herbaria and libraries under their charge. She greatly appreciates the efforts of a large number of botanists and collectors, resident in Africa, who specially collected and supplied material.

I. INTRODUCTION

Terminalia is a pantropical genus in the almost exclusively tropical family Combretaceae. The last monograph of the family to cover the whole world is that of De Candolle (*Prodromus*, **3**), published in 1828. Since then our knowledge of the family has been greatly increased, but most accounts deal only with restricted regions.

Exell (*J. Bot., Lond.*, **69**, 113–28, 1931) gives a brief historical account of the family and provides a key to the genera based on that of Engler and Diels (*Monogr. Afr. Pflanzenfam. u. Gatt.*, **3**, *Combretaceae–Combretum* (1899)), but with a few important modifications. The major synonymy and an outline of distribution of the genera is given; that of *Terminalia* which has many synonyms is particularly valuable. He accepts *T. catappa* L. as being the type of the genus as it is the only species represented in the Linnean herbarium. The name *Terminalia* has been conserved against *Adamaram* Adans.

Terminalia in Africa was monographed by Engler and Diels in 1900 (*Monogr. Afr. Pflanzenfam. u. Gatt.*, **4**, *Combretaceae excl. Combr.*) and has not been revised since. The material available at that time was very limited, and some of their species were based on single gatherings. Since then, a number of botanists have published works dealing with a few isolated species or with the species of a particular part of Africa. Some of Engler and Diels's species have been reduced to synonymy, and a number of additional species have

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been described. The treatments in different regional floras and hand-books do not always correspond, and there is no later work that effectively deals with the species of South Tropical Africa. Much more material is available to-day than the German authors had access to, and the time for a revision is long overdue.

One hundred and fifteen specific names referring to African species have been published, and all are accounted for in the Appendix; a few of these are *nomina nuda* and illegitimate, but most were described as species. Fifty-five names are dealt with by Engler and Diels in their monograph; forty-four apply to species they maintain and describe; the remaining eleven were treated as synonyms. Four species (*T. albida, brandisii, confertifolia* and *randii*) published before this monograph are not mentioned. A further fifty-five names have been published during the present century. One of them *T. glandulipetiolata*) is based on cultivated material of the asiatic *T. chebula*; the others refer to indigenous species.

In this account only twenty-eight species are regarded as being sufficiently well-known to merit a full treatment, and it appears likely that when the flora of tropical Africa is more completely known than it is to-day the total number of acceptable species will not greatly exceed that figure. A further twelve entities are treated as 'imperfectly known species' at the appropriate places in the text (pp. 845, 849, 858, 870 and 891). Seven of these (*T. mangela, robecchii, salicifolia, silozensis, somalensis, trichopoda* and *verdickii*) already have names, but the available material and information is insufficient to provide a basis for a decision as to their correct status. It is possible that some of these imperfectly known species may represent good species, but conclusive evidence, at the time of writing, is lacking.

Engler published eleven new names in *Die Pflanzenwelt Afrikas* (1921), but indicated no type-specimens, and if they ever existed they are certainly now destroyed. From the scanty information provided it is impossible to assess their relationships, and, apart from mentioning them in the Appendix, ten of them (*T. bagamoyoana, chrysomalla, dielsii, emarginata, foetens, laeteviridis, morogoroensis, mpwapwensis, roseogrisea* and *tristis*) are not dealt with here; the eleventh species, *T. flava*, is represented in the Kew herbarium by material distributed from Berlin, and is regarded as a synonym of *T. glaucescens*.

Eleven species (*T. bispinosa, canescens, dolichocarpa, hararensis, hecistocarpa, holtzii, mildbraedii, poliotricha, riparia, splendida* and *thomasii*) were described by various German authors, and although type specimens were cited they are now destroyed. It has not been possible to establish their identity from the descriptions alone. Further information about them is recorded in the Appendix.

The type specimens of 3 other species (*T. balladellii, basilei, obovata*) have not been located.

Only a few species show characters which are *absolutely diagnostic* among the African species; in other words, have one or more characters shown by every individual of the species and not shared by any other species. *T. superba*, alone among the African species, has a transversely oblong fruit, but this character is shared by a few tropical Asian and American species. So far as is known, no African species possesses a single diagnostic character which is valid within the genus as a whole. This means that the species must be distinguished by sets of closely correlated characters. Great care must be taken in grouping species for purposes of classification and in keys when this is the case. Artificial keys, which have been so much used in the early stages of taxonomy, and which are often based primarily on such characters as linear dimensions, and the amount and distribution of the indumentum, lead for the most part to artificial groupings of the species, and often rapidly become unworkable when more material is collected. The keys in Engler and Diels's *Monograph* have these defects.

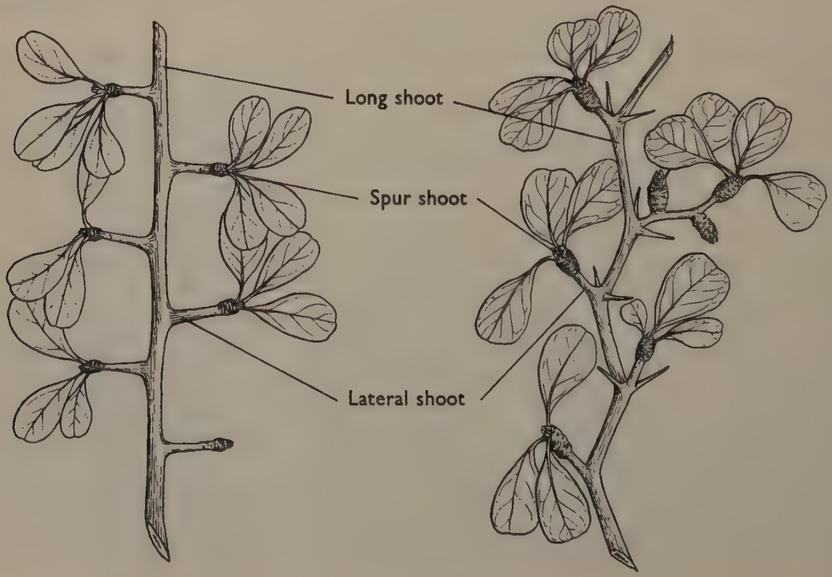
The key in the present work is entirely original. An attempt has been made to produce a key in which the major groupings are natural and based, as far as possible, on a number of correlated characters, so that closely related species key out near to each other, and are not widely separated, as they often are in artificial keys. In separating the members of pairs (or larger groups) of species in the final dichotomies of the key a large number of characters has frequently been used. The chief reason for this is that although most species are not difficult to recognize, perfectly diagnostic characters are few or absent, and the specimen being identified may be incomplete and so not show them. For most species identification is more a matter of considering a relatively large number of *differential* characters and making an assessment of their correlation. This is because most of the best characters available for separating species, taken singly, overlap slightly. When all such differential characters are considered collectively the resulting diagnosis is absolutely diagnostic. Specimens may be found which are atypical for one, or possibly two, of the many characters which contribute to the diagnosis, and because these characters appear to vary independently it is necessary to use a large number. Genuine intermediates between most species appear to be very rare (except in the *T. sericea* group) and, where they have been detected, attention is drawn to them in the appropriate places in the text. Where species are distinguished in the key by few characters it means that they are closely related and few characters are available for this purpose.

In the manner of branching and in the arrangement of the leaves, the African species fall into two easily recognized and very natural groups, and these characters have been used in the first big division of the Key. Engler and Diels placed the African species in five sections (Myrobalanus, Discocarpae, Bialatae, Stenocarpae, Platycarpae), based mainly on the shape and proportions of the fruit. Two of their sections (Stenocarpae and Platycarpae) are artificial, and it is not surprising to find that the members of one of them fall into both of the major groups adopted in the key used here.

Synonymy and references to literature

For each species synonymy is given in full, and that which is new is indicated. An attempt has been made to include references to all taxonomic works that include descriptions and records of the African species of *Terminalia*, where specimens are cited. In addition, references are also given to Engler's account in *Die Pflanzenwelt Afrikas*, although no specimens are cited.

Branchlets. The meanings of the terms 'long shoot', 'lateral shoot' and 'spur-shoot' are illustrated below.



Leaves. The measurements given in the key and descriptions are taken from well-developed leaves of flowering and fruiting specimens. All abnormal and immature leaves have been ignored. The type of indumentum is sometimes important in distinguishing closely related species, for instance, the short curly hairs of *T. avicennioides* and the long silky hairs of *T. albida*. The indumentum of the former can be easily rubbed off; that of the latter cannot. In *T. mollis*, *T. stenostachya*, *T. glaucescens* and the pubescent form of *T. laxiflora* the indumentum can also be rubbed off.

Flowers. Apart from differences in size and indumentum, the flowers are remarkably uniform in structure, and offer few features of diagnostic value. The calyx-lobes, however, may be either erect or spreading, or reflexed in the open flower. Reflexed calyx-lobes are confined to the sections *Discocarpae* and *Bialatae*. The shape of the calyx-lobes —obtuse, acute or acuminate—is the only morphological character of the flower included in the descriptions. For some species it serves as a useful supplementary character (see Figs. 22 and 23, *T. avicennioides* and *T. albida*).

Fruits. The fruits provide many characters for distinguishing species, but in Africa the total range of variation is much less than that shown by Asiatic species (see Exell, *Fl. Malesiana, Combretaceae*, pp. 572–582, tt. 14, 22, 24, 25 and 29). Except for *T. fatraea*, all African species have two wings (*T. orbicularis* occasionally has 3–4 wings, but this is not normal for the species). *T. fatraea*, *T. orbicularis*, *T. scutifera* and *T. superba* can be identified by the fruits alone (see key).

Illustrations. For each of the twenty-eight species which are treated in full a plate of illustrations has been drawn. These should serve to illustrate and amplify the key and specific descriptions, besides showing something of the habit and general facies of the species. All illustrations have been drawn to the same scale: flowering and fruiting branchlets, $\times \frac{1}{2}$; flower buds, $\times 4$; opening flower, $\times 5$; open flower, $\times 4\frac{1}{2}$; longitudinal section through open flower, $\times 4\frac{1}{2}$. Only flowers at a comparable stage of development were chosen for illustration; flower buds and opening flowers were taken from a quarter of the way along the spike from the apex; open flowers at the stage when the lower receptacle is beginning to lengthen as the fertilized ovule develops. Indumentum has not been shown on the drawings of flowering and fruiting branchlets, but has been shown in detail for the flower drawings.

Citation of specimens. About 1400 specimens have been examined, and this comprises all the material, so far as is known, in the following herbaria: BM, BR, BRLU, EA, FHO, K, OXF, SRGH. In addition, type specimens were obtained on loan from Florence, Zurich, Paris and Uppsala; these were photographed; one set of prints is housed in the Forest Herbarium, Oxford (FHO) and another has been sent to Kew. A short time before this revision was started, Forest Departments in all the African territories administered by the Colonial Office and a number of botanists resident in Africa were asked to supply material. Much valuable material was obtained in response to these requests.

Information about all specimens examined was recorded on cards, but only five specimens (when available) have been cited for each territory. This is considered adequate to cover the range of variation and geographical distribution. More than five specimens are cited only when there are several type specimens (including those of synonyms) from a territory. The specimens selected for citation include all type material that has been examined and all specimens used for the illustrations.

Distribution and ecology

So far as is known, no ecological study dealing specifically with *Terminalia* in Africa has ever been made. Nevertheless, a great deal of ecological information has been recorded by numerous authors in more general accounts of the vegetation of restricted areas. This can often be supplemented by observations recorded on labels accompanying herbarium specimens. An attempt has been made to bring together all these scattered observations, species by species. The sources from which the data were obtained are listed in a bibliography at the end of the paper. Fig. 29 is a map which shows the distribution of all the African species, in so far as they can be assessed from herbarium specimens. In section IV a few generalizations of ecological and phytogeographical interest are made, but it must be emphasized that more field work and collecting is necessary before a more complete picture will emerge.

Abbreviations of herbaria

These are taken from *Index Herbariorum*, ed. 3, *Regnum Vegetabile*, **6**, (1956). SGH—Sudan Government Herbarium, Wad Medani, is not included in the above.

Abbreviations of references

The following, frequently cited work, is abbreviated more than is customary: Engl. & Diels, *Monogr.* **4** = Engler and Diels, *Monographieen Afrikanischer Pflanzenfamilien und Gattungen*, **4**, *Combretaceae excl. Combretum*, Leipzig (1900).

II. KEY TO THE AFRICAN SPECIES

GROUP I. Leaves in fascicles terminating short spur-shoots of very slow growth; branchlets and branches often spinous:

1. Frt. wingless, 1–1·2 × 0·5 cm., ellipsoid-ovoid, apex and base acute; fls. with obscurely ridged lower receptacle and irregularly lobed disc (Sect. **Myrobalanus**). **1.** *T. fatraea*

1*a*. Frt. with 2 (v. rarely in *T. orbicularis* with 3–4) wings:

  2. Lvs. suborbicular, petiole 2–6 cm. long; frt. suborbicular, 6·5–9 × 5·5–8·5 cm., wings broad, developed beyond style at apex and beyond insertion of pedicle at base; calyx-lobes reflexed in open fls. (Sect. **Discocarpae**). **2.** *T. orbicularis*

  2*a*. Lvs. not suborbicular, petiole v. rarely more than 2 cm. long; frt. not suborbicular, always less than 6 × 3 cm., wings not developed beyond style and insertion of pedicel; calyx-lobes erect (Sect. **Platycarpae**, p.p.):

    3. Long shoots straight or almost so:

      4. Lateral shoots inserted ± regularly along long shoot, about 4–6 cm. apart, diverging almost at right angles, ending in a spur-shoot; spur-shoots very rarely borne directly on long shoots; spines, when present only on long shoots; frt. elliptic-oblong, 4–6·5 × 2–2·9 cm. **3.** *T. prunioides*

      4*a*. Lateral shoots scattered irregularly along long shoot and diverging at obtuse angle, ending in a spine and bearing 1–3 spur-shoots; spur-shoots and spines often borne directly on long shoot; frt. suborbicular, 1·8–2·4 × 1·9–2 cm. **4.** *T. brevipes*

      4*b*. Lateral shoots scattered irregularly along long shoot and diverging at obtuse angle, ending in a spur-shoot (rarely in a spine) and bearing 10–15 (or more) spur-shoots; numerous spur-shoots also borne directly on long shoot; spines never present on long shoots; frt. ovate-elliptic, 1·8–2 × 1·2–1·4 cm. **5.** *T. parvula*

    3*a*. Long shoots zigzag:

      5. Lower receptacle and frt. glab.; spines present:

        6. Lvs. scarcely longer than broad, broadly obovate, the largest lvs. on fertile specimens never less than 2 cm. broad, apex rounded to subtruncate and deeply emarginate, base longly cuneate (E. Trop. Afr.). **6.** *T. spinosa*

6*a*. Lvs. much longer than broad, oblanceolate to narrowly obovate, less than 2 cm. broad, apex obtuse, slightly emarginate or mucronate:
7. Lvs. never greater than 2·5 cm. long, pale green, nerves on both surfaces scarcely visible; infl. up to 3·5 cm. long; frt. up to 2·5 cm. long; spines present at base of most spur-shoots (S. Trop. Afr.). **7.** *T. randii*
7*a*. Lvs. usually greater than 4 cm. long, glaucous-green above, pale yellowish green beneath, secondary nerves raised above, inconspicuous beneath; infl. greater than 5 cm. long; frt. greater than 2·5 cm. long; spines rarely present at base of spur shoots (E. & S. Trop. Afr.). **8.** *T. stuhlmannii*
5*a*. Lower receptacle tomentose; frt. finely puberulous; spines absent. **9.** *T. polycarpa*

Group II. Leaves not in fascicles terminating short spur-shoots, usually scattered, but sometimes more or less crowded towards the ends of lateral shoots; spines absent:

(A). Bark on young branchlets purple-black, excorticating in papery flakes; newly exposed surface reddish brown, finely striated, becoming grey-brown in second year (Sect. **Platycarpae**, p.p.):

8. Lvs. less than twice as long as broad, densely sericeous-tomentose on both surfaces. **10.** *T. erici-rosenii*
8*a*. Lvs. glab. or pubescent, if sericeous-tomentose then greater than 3 times as long as broad:
9. Lvs. completely glab. (at least when mature):
10. Lvs. sessile. **11.** *T. brachystemma*
10*a*. Lvs. distinctly petiolate, petiole 1–3·5 cm. long. **12.** *T. kaiserana*
9*a*. Lvs. pubescent to sericeous-tomentose:
11. Lvs. ± lyrate, subamplexicaul at base. **13.** *T. sessilifolia*
11*a*. Lvs. cuneate at base. **14.** *T. sericea*

(B). Bark on branchlets various, not peeling as above:

12. Frt. sessile, broader than long; calyx-lobes reflexed in open fls.; style hairy, coastal and high forest species (Sect. **Bialatae**):
13. Petiole less than 2 cm. long; infl. up to 8 cm. long; lower receptacle densely ferrugineous-tomentose; frt. subrhomboid (coastal species). **15.** *T. scutifera*
13*a*. Petiole 3–7 cm. long; infl. greater than 10 cm. long; lower receptacle densely sericeous-tomentose; frt. transversely elliptic-oblong (high forest species). **16.** *T. superba*
12*a*. Frt. distinctly pedicellate, longer than broad; calyx-lobes erect or spreading in open fls.; style hairy or glab. (savannah woodland species, except *T. ivorensis*):
14. Branchlets becoming corky in second year, later developing a thick layer of cork (Sect. **Stenocarpae**, p.p.):
15. Lvs. sessile or occasionally shortly petiolate, if so then lamina decurrent almost to base of petiole. **17.** *T. macroptera*
15*a*. Lvs. distinctly petiolate, petiole 2–5 cm. long, lamina not decurrent:
16. Lvs. usually 16–22 cm. long, 6–8 cm. broad, venation on lower surface, obscurely reticulate, not prominent; frt. glab. (at least when mature), 5·7–8 × 2·6–3·5 cm.; fls. glab., pubescent or tomentose. **18.** *T. laxiflora*
16*a*. Lvs. 16–32 cm. long, 7–11 cm. broad; venation on lower surface conspicuously reticulate, prominent or subprominent; frt. densely velutinous-tomentose, even when mature, 6·5–11·5 × 2·8–5·5 cm.; fls. always densely tomentose. **19.** *T. mollis*

KEY TO THE AFRICAN SPECIES (*cont.*)

14*a*. Branchlets remaining fibrous after several years' growth:

17. Frt. narrowly oblong, at least 3 times as long as broad (Sect. **Stenocarpae**, p.p.):

18. Forest species with tall, straight bole; lvs. abruptly and shortly acuminate, usually 10·5–13·5 × 4·5 cm., almost glab.; frt. 5·8–10 × 1·7–2 cm. (W. Trop. Afr.). **20.** *T. ivorensis*

18*a*. Savannah woodland species with short, frequently gnarled bole; lvs. mostly 15–22·5 × 5–8 cm. (occasionally larger), sparsely to densely sericeous-tomentose on main nerves beneath; frt. 5·5–7·5 × 1·5–2·2 cm. (W. and E. Trop. Afr.). **21.** *T. glaucescens*

17*a*. Frt. always much less than 3 times as long as broad (Sect. **Platycarpae**, p.p.):

19. Indumentum of lvs. either of very short curly hairs (giving a felted appearance), or of closely appressed silky hairs; lower and upper receptacle densely tomentose; frt. tomentose when mature:

20. Lvs. loosely velutinous-tomentose beneath with curly hairs, drying brown, upper surface matt; frt. densely velutinous-tomentose. **22.** *T. avicennioides*

20*a*. Lvs. appressed sericeous-tomentose beneath, upper surface shining; frt. densely sericeous-tomentose. **23.** *T. albida*

19*a*. Indumentum of lvs. of spreading hairs; lower receptacle glab. to densely tomentose (if appressed then not silky); upper receptacle glab., or tomentose only at base; frt. glab. or minutely puberulous when mature:

21. Older branchlets with very prominent leaf-scars; apical bud conspicuous, silver-grey, about 0·7 × 0·7 cm.; lvs. elliptic to elliptic-oblong, apex rounded to acute (very rarely shortly acuminate); fls. densely tomentose with spreading hairs. **24.** *T. stenostachya*

21*a*. Older branchlets and apical buds not as above; lvs. ± broadly obovate to elliptic-obovate, apex shortly acuminate or cuspidate; fls. glabrous or densely tomentose with appressed hairs:

22. Fls. and frt. glab.:

23. Frt. 2·5(–3) × 1·7–2 cm., base rounded or subtruncate. **25.** *T. gazensis*

23*a*. Frt. 3·5–5 × 2·3–2·5 cm., base acute or obtuse. **26.** *T. brownii*

22*a*. Fls. densely tomentose; frt. minutely puberulous:

24. Tertiary nerves and veins scarcely impressed above; frt. (6–)7–8·5 × 3·5–3·8 cm. (E. and S. Trop. Afr.). **27.** *T. kilimandscharica*

24*a*. Tertiary nerves and veins conspicuously impressed above; frt. 2·8–4 × 1·8–2·7 cm. (S. Afr. and Port. E. Afr.). **28.** *T. phanerophlebia*

III. Descriptions of the African species

(1) **Terminalia fatraea** (Poir.) DC., *Prod.* **3**, 12 (1828); Tul., *Ann. Sci. Nat.* (4), **6**, 95 (1856); Engl., *Pflanzenw. Ost.-Afr.* **C**, 295 (1895); Engl. & Diels, *Monogr.* **4**, 9, t. 15D (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 718 (1921); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr.), **2**, 143 (1949).

Mirobalanus fatraea Poir., in *Encycl. Bot.*, Suppl. **3**, 708 (1824).
T. madagascariensis Spreng., *Syst. Veg.* **2**, 358 (1825).

See Fig. 1. Much-branched shrub or small tree, 5–8 m. high; bark of bole smooth, greyish brown; bark of branchlets purplish brown to light brown, fibrous. Long shoots straight, with lateral shoots diverging at obtuse or acute angle. Lateral shoots terminating in a spur-shoot and bearing 4–6 lateral spur-shoots 0·2–0·5 cm. long. Many spur-shoots are also borne directly on long shoot. *Lvs.* oblanceolate to narrowly obovate, apex obtuse to rounded, occasionally shortly subacuminate, base acute to cuneate, 2·5 × 1–6 ×

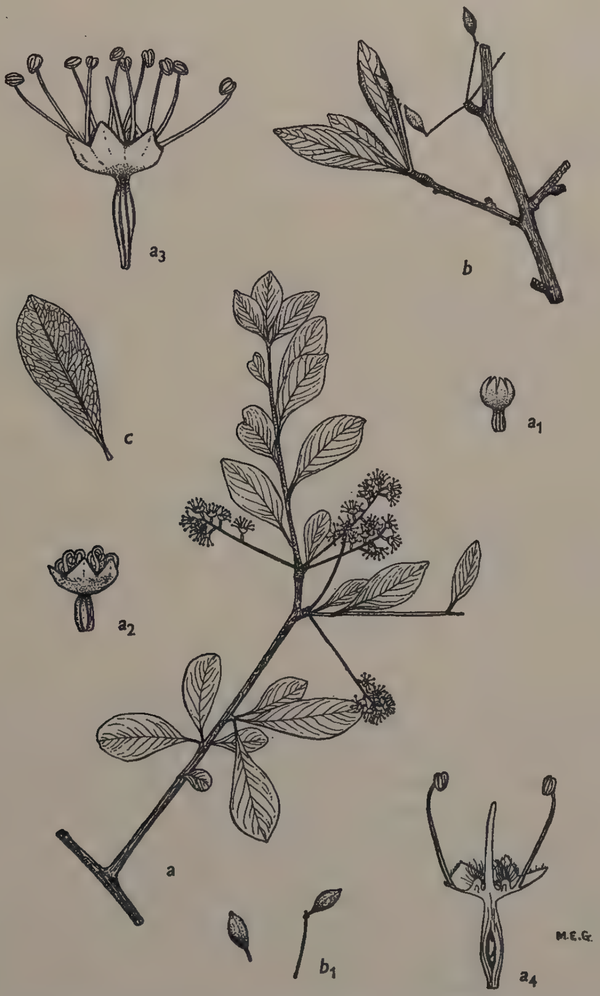


Fig. 1. *T. fatraea* (Poir.) DC. *a*, a_3–a_4, from *Vaughan* 2029; a_1, a_2, from *Bojer* s.n.; *b* from *Greenway* 5062; b_1, *c*, from *Greenway* 5049.

1·5 cm., glabrous, revolute, chartaceous, pale green and shining above, paler green and dull beneath, midrib impressed above, prominent beneath, secondary and tertiary nerves raised above, subprominent beneath; petiole 0·2–0·5 cm. long. *Infl.* 2·5–3·5 cm. long, peduncle 1·5–1·8 cm. long, glabrous; *fl.* glabrous or very sparsely pilose, lower receptacle obscurely ridged; calyx-lobes obtuse; disc with 5–7 irregular lobes. *Frt.* ellipsoid-ovoid, apex and base acute, 1–1·2 × 0·5 cm., wings or ridges absent, glabrous, pale yellowish green; pedicel 0·2–0·3 cm. long.

T. fatraea shows only slight variation in leaf-size and shape. In contrast to most *Terminalia* species the form of the fruits is remarkably uniform.

KENYA. Kilifi Dist., Mida, fl., Oct. 1930, *Donald* 2496 (EA, K), medium-sized tree, 0·76 m. girth. Id., Kilifi, in thicket nr. shore, st., July 1937, *Moggridge* 415 (EA, K). Digo Dist., Mombasa, frt., Nov. 1884, *Rev. T. Wakefield* s.n. (K).

TANGANYIKA TERRITORY. Lindi Dist., Sudi, fl., Dec. 1942, *Gillman* 1174 (EA), small tree in 'Mpande'-'Mkungni' community, in secondary thicket on reddish sands. Kisarawe Dist., Pugu F. R., nr. Kisarawe, fl., June 1954, *Semsei* 1716 (EA), small tree with white fls. Bagamoyo Dist., Bagamoyo, frt., *Stuhlmann* 8017 (EA).

PEMBA ISLAND. Nr. Ngugu, frt., Feb. 1929, *Greenway* 1447 (EA, K), small, much-branched tree, on sea-shore above high-water mark.

ZANZIBAR. Kiwengwa to Kinyasini, frt., Jan. 1929, *Greenway* 1246, st., 1247 (EA, K), common, much-branched tree 5–7 m. high, in closed bush formation on coral rocks nr. coast. No locality given, fl., Oct. 1861, *Kirk* s.n. (K). Chwaka, frt. (immature), Dec. 1930, *Vaughan* 1784 (EA, K), in bush, tall shrub. Mazizini Beach, just above high-water mark (also found in east coast bush), fl., Dec. 1932, *Vaughan* 2029 (BM, EA, FHO), shrub with yellow fls.

MAFIA ISLAND. Kange, alt. 3 m., frt., Aug. 1937, *Greenway* 5049 (EA, FHO, K), locally dominant in *Diospyros–Pemphis–Mimusops–Sophora* association on a sand-bank in *Ceriops–Rhizophora* mangrove formation; much-branched shrub or small evergreen tree up to 6 m. high, bark smooth, greyish brown. Bweni to Ras Mkumbi, alt. 13 m., frt., Aug. 1937, *Greenway* 5062 (EA, FHO, K), much-branched evergreen tree 8 m. high, on brown soil on coral rock formation, co-dominant with *Sideroxylon*, *Grewia*, *Flacourtia* and *Ludia*, in evergreen bush.

PORTUGUESE EAST AFRICA. Niasa Prov., Msalo R., *Allen* 96, fl. (K), wood very hard, used in boat-building in place of nails, hence vernacular name (*Somari*) which means nails.

MADAGASCAR. Central Madagascar, fl., frt., *Rev. R. Baron* 2237 (BM, K). No locality or date given, fl., *Bojer* s.n. (OXF). Fort Dauphin, fl., *Cloisel* 792 (BM) shrub with pale yellow fls., growing nr. the sea. Id., *Scott Elliot* 3048 (BM), in woodland.

Taxonomic history

The taxonomic history of *T. fatraea* is very confused, but the situation appears to be as follows: Poiret cites '*Fatraea madagascariensis* Juss. in Herb.' as a synonym of *Mirobalanus fatraea*, therefore, presumably he based his species on the former, which seems never to have been validly published. Poiret does not cite any type material, but the latter would appear to be located in Herb. Jussieu (not seen). Sprengel cites *M. fatraea* as a synonym of his species *T. madagascariensis* without any explanation and does not mention the specimens on which the latter was based.

H. Perrier de la Bâthie (*Fl. Madagascar et des Comores*, **151**, 68 (1954)) cites *T. fatraea* as a synonym of *T. pumila* Thouars ex Tul. (*Ann. Sci. Nat.* **6**, 77 (1856)), although *T. fatraea* is the earlier name (there are 27 species of *Terminalia* on Madagascar, all of which were described after *T. fatraea*). He does not give any reasons for this synonymy, and, in addition, mentions *T. pumila* as being endemic to Madagascar, which implies that '*T. fatraea*' is also endemic to this island!

In the present author's opinion, the plant previously known in East Africa as *T. fatraea* also occurs on Madagascar (see citations above); she has not had the opportunity to decide whether Perrier's views on the nomenclature of this species are justified.

Distribution and ecology

A species of very limited distribution occurring only on Madagascar, Zanzibar, Pemba and Mafia islands and along the coastal districts from Kenya to Portuguese East Africa.

In Kenya (8) it is one of the commonest shrubs in the dense bush between Kilifi and Roka where the drainage is good; the annual rainfall is between 750 and 1000 mm. (30–40 in.).

On Zanzibar it also occurs in the evergreen or partially evergreen forest area of the western side of the island.

(2) **T. orbicularis** Engl. & Diels, *Monogr.* **4**, 26, t. 15 A (1900), incl. var. *macrocarpa* Engl. & Diels; Engl., *Pflanzenw. Afr.* **3** (**2**), 726 (1921).

T. praecox Engl. & Diels, *op. cit.* 27, t. 15 C; Engl., *op. cit.* 726; Chiov., *Fl. Somala*, **1**, 172 (1929), **2**, 201 (1932), synon. nov.

T. ruspolii Engl. & Diels, *op. cit.* 26, t. 15 B. Pampan., *Bull. Soc. Bot. Ital.* p. 18 (1915) (var. *macroptera* Pamp.); Engl., *op. cit.* 726; Chiov., *op. cit.* 172 (1929), *op. cit.* 207 (1932), synon. nov.

See Fig. 2. Large spreading shrub 3 m. high, or small tree up to 7 m. high with irregularly diverging branches or straight branches set at right angles; bole often very short, 0·7–1·3 m. high; bark of bole smooth, grey; bark of branchlets reddish purple to purplish grey with fine longitudinal fissures. Long shoots zigzag, with lateral shoots diverging at acute angle and ending in a spur-shoot. *Lvs.* suborbicular, apex broadly and shortly acuminate, mucronate or emarginate, base rounded to subcordate, occasionally decurrent, 6·5 × 4·2–13·5 × 7·5 cm., glabrous, chartaceous, pale green, midrib and secondary nerves and venation ± conspicuous on both surfaces; petiole 2–6 cm. long. *Infl.* 3·5–5 cm. long, peduncle 0·7–1 cm. long, densely tomentose; *fl.*: lower receptacle densely tomentose, upper receptacle tomentose only at base; calyx-lobes acute, bright purplish red, reflexed in open fl. *Frt.* suborbicular, wings usually 2, but occasionally up to 4, developed beyond style at apex and beyond insertion of pedicel at base, projections frequently overlapping, apex rounded, base deeply cordate, 6·5 × 5·5–9 × 8·5 cm., finely puberulous, greenish to bright crimson; pedicel 0·7 cm. long.

All the available material consists of fruiting, often leafless, specimens, except for two flowering specimens. The specimens with leaves show no appreciable variation in leaf-shape, and only slight differences in size. The fruits are, however, extremely variable and the two extremes are those which caused Engler and Diels to make two species, viz. the difference in the apex of the fruits—see below under 'taxonomic history'.

Ethiopia. Ogaden, reserved area 60 km. E. of Awareh, alt. 930 m., frt., Oct. 1954, *Bally* 10130 (K), in *Commiphora* association on red sandy soil; spreading bush 2·7 m. high, 3 m. diam., with stiff branches. Precise locality not given, frt., Dec. 1894, *Donaldson Smith* 304 (BM). Ogaden, 32 km. from Wardere on Shilarvi Rd., alt. 800 m., frt., Oct. 1953, *Ellis* 147 (K), tree 7 m. high with drooping branches, shiny leaves and red frt.; on red sandy soil, very common in wetter parts. Id., Harradigit, alt. 981 m., frt., Nov. 1934, *Godding* 236 (K), tree with bright red frt.

British Somaliland. Bohotle, alt. 700–1000 m., frt., Dec. 1933, *Gillett* 4718 (K), in *Commiphora*, bush–*Acacia* formation; small tree with light pink frt. produced profusely when tree is leafless giving a very striking effect. Nr. Bohotle, frt., Oct. 1944, *Glover & Gilliland* 259 (EA), frequent tree, 3–7 m. high with large greenish to bright crimson frt.; just coming into leaf. Halkulan Tug, Karin, nr. Berbera, alt. 116 m., frt., *Glover &*

Gilliland 1184 (EA, K), on rocky tug bed, rare tree 3·5 m. high. Ainabo, alt. 1000 m., frt., Sept. 1941, *Capt. Peck* 347 (EA, K), tree 5–7 m. high, leaves present only in rains for a short time and then browsed by goats and camels.

ITALIAN SOMALILAND. 19 km. S. of Iscia Baidoa, fl., frt., Sept. 1951, *Bond & Pechanec* 20 (EA). 31 km. N. of El Bur, frt., Oct. 1951, *Bond & Pechanec* 43 (EA). Uebi Valley, frt., July–Aug. 1891, *Robecchi Bricchetti* 232 (FI, holotype of *T. orbicularis* var. *macrocarpa* Engl. & Diels). Id., in dry bushy places, frt., Jan. 1893, *Ruspoli & Riva* 118, 912 (FI, syntypes of *T. ruspolii*).

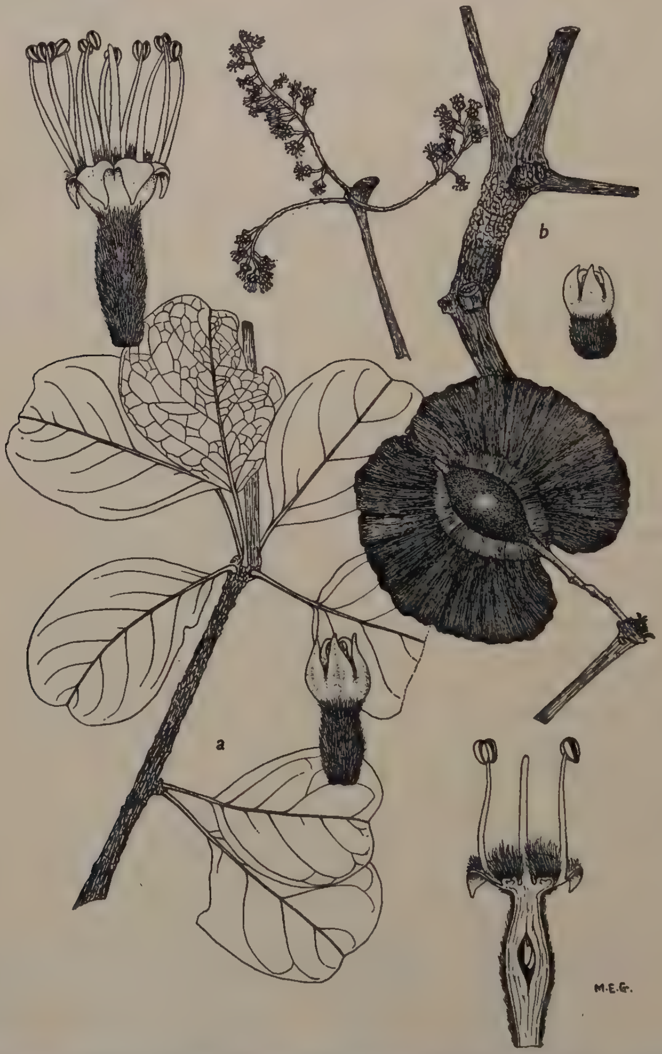


Fig. 2. *T. orbicularis* Engl. & Diels. Flowering specimen from *Braun* 1539. Fruiting specimen from *Dale* 3896. *a*, from *Glover & Gilliland* 1184; *b*, from *Bond & Pechanec* 43.

KENYA. Northern Frontier Dist., Matthew's Range, Olkanto, alt. 1000 m., frt., Dec. 1944, *Mrs Joy Adamson* 52 (K), common large tree. Tana River Dist., Bura, frt., Jan. 1947, *Mrs Joy Adamson* 359 (K), much-branched bushy tree. Teita Dist., nr. Voi, fl., Mar. 1907, *Braun* 1539 (EA), tree 5–6 m. high, leafless. Id., Ndi, nr. Voi, frt., Jan. 1938, *Dale* 3896 (EA, K), in 'Nyika' bush, shrubby tree 4 m. high, ripening frt. rose-pink. Northern Frontier Dist., Dandu, alt. 830–1000 m., Mar. 1952, mature leaves (beginning to fall), May 1952, fl., frt., *Gillett* 12559 (K, neotype), shrub 4 m. high with fragrant fls., perianth crimson outside, cream within; confined to immediate foot of mountain, well drained but water supply increased by run-off from mountain; frequent in this one type of habitat.

Taxonomic history

Engler and Diels based *T. orbicularis* on a leafless fruiting specimen (*Hildebrandt* 2607, now destroyed); their variety *macrocarpa* (*Robecchi Bricchetti* 232!) was alleged to differ only in having wider fruits (*T. orbicularis* 6–7·5 cm. broad, var. *macrocarpa* 8–9 cm. broad); *T. ruspolii* was based on three leafless fruiting specimens (*Ruspoli* and *Riva* 118!, 912! and *Pospischil* s.n.), which differ from *T. orbicularis* in having smaller fruits with overlapping apical projections. There is considerable variation in the size of the fruits and in the degree of overlapping of these apical projections even on the same specimen, so that *T. ruspolii* cannot be maintained; size of fruit is too variable a character to make the variety worth retaining.

T. praecox was based on a flowering specimen (*Thomas* 60) with very young leaves. Although the type specimen has not been seen, there is little doubt that *T. praecox* is none other than the flowering stage of *T. orbicularis*. *Gillett* 12559 (with fls. and frt.) is a good match for the description and illustration of *T. praecox*; it also matches a flowering specimen (*Braun* 1539) named *T. praecox*, which was deposited at Amani when Tanganyika was administered by Germany, and had probably been compared with the type.

Distribution and ecology

T. orbicularis is distributed from British Somaliland through the Ogaden in eastern Ethiopia to central and southern Italian Somaliland, and southwards to southern Kenya. It occurs, therefore, in the *Acacia*, desert–grass savannah region, where *Acacia* and *Commiphora* spp. predominante; this occupies areas with an annual rainfall of about 250 mm. (10 in.).

(3) **T. prunioides** Laws., *Fl. Trop. Afr.* **2**, 415 (1871); Engl. & Diels, *Monogr.* **4**, 22, t. 2A (1900); Engl. & Gilg, in Warb., *Kunene-Sambezi Exped.* p. 322 (1903); Schinz, Plant. Menyhart., in *Denkschr. Akad. Wiss. Wien*, **78**, 431 (1905); Lugard & N. E. Brown, *Kew Bull.* p. 110 (1909); Engl., *Pflanzenw. Afr.* **3** (2), 725 (1921); Burtt Davy, *Man. Fl. Trees & Shrubs Transv.* **1**, 250 (1926); Obermeyer, Schweickerdt & Verdoorn, *Bothalia*, **3**, 247 (1937); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, **2**, 149 (1954).

T. porphyrocarpa Schinz, *Verh. bot. Ver. Brandenb.* **30**, 242 (1888); non *T. porphyrocarpa* F. Muell. ex Benth. (1864).

T. rautanenii Schinz, *op. cit.* 243; Engl. & Diels, *op. cit.* 22, t. 10B; Engl., *op. cit.* 725; Obermeyer *et al.*, *op. cit.* 247, synon. nov.

T. holstii Engl., *Abh. preuss. Akad. Wiss.* p. 34 (1894); Engl., *Pflanzenw. Ost-Afr.* **C**, 294 (1895); Engl. & Diels, *op. cit.* 23, t. 11B; Engl., *op. cit.* 725; Chiov., *Fl. Somala*, **1**, 172 (1929), **2**, 207 (1932); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr.), **2**, 145 (1949), synon. nov.

T. petersii Engl., *op. cit.* 294 (1895).

T. benguellensis Welw. ex Hiern, *Cat. Afr. Pl. Welw.* **2**, 339 (1898), incl. var. *ovalis* Hiern; Engl. & Diels, *op. cit.* 23 synon. nov.

See Fig. 3. Shrub 2–4 m. high or small tree 7–15 m. high, with rounded crown; bark of bole longitudinally fissured, grey; slash yellow; bark of branchlets fibrous, purplish brown to grey. Long shoots straight, with ± regularly arranged lateral shoots, about 4–6 cm.

apart and diverging almost at right angles. Lateral shoots ending in spur-shoot 0·7–1·5 cm. long, very rarely bearing additional lateral spur-shoots. Spur-shoots rarely borne directly on long shoot. Spines occasionally present, about 2 cm. long, present on long shoots only. *Lvs.* broadly obovate to elliptic-obovate, apex rounded, emarginate or mucronate, base obtuse to cuneate, 1·75 × 1·5–7·5 × 3 cm., sparsely pubescent, often becoming ± glabrous, chartaceous; *upper surface*: midrib and secondary nerves ± impressed, tertiary nerves and venation scarcely visible; *lower surface*: midrib prominent, secondary nerves subprominent, tertiary nerves inconspicuous, venation finely and obscurely reticulate; petiole 0·5–1·5(–2·5) cm. long. *Infl.* 5–8 cm. long, peduncle 1·7–2 cm. long, sparsely pubescent; *fl.* glabrous or lower receptacle very sparsely pubescent; calyx-lobes subacute. *Frt.* elliptic-oblong, apex obtuse, deeply emarginate or mucronate, base obtuse to cuneate or subtruncate and then slightly decurrent, 4 × 2–6·5 × 2·9 cm., wings sometimes puckered at margin, glabrous, purplish brown or bright red; pedicel ± 0·7 cm. long.

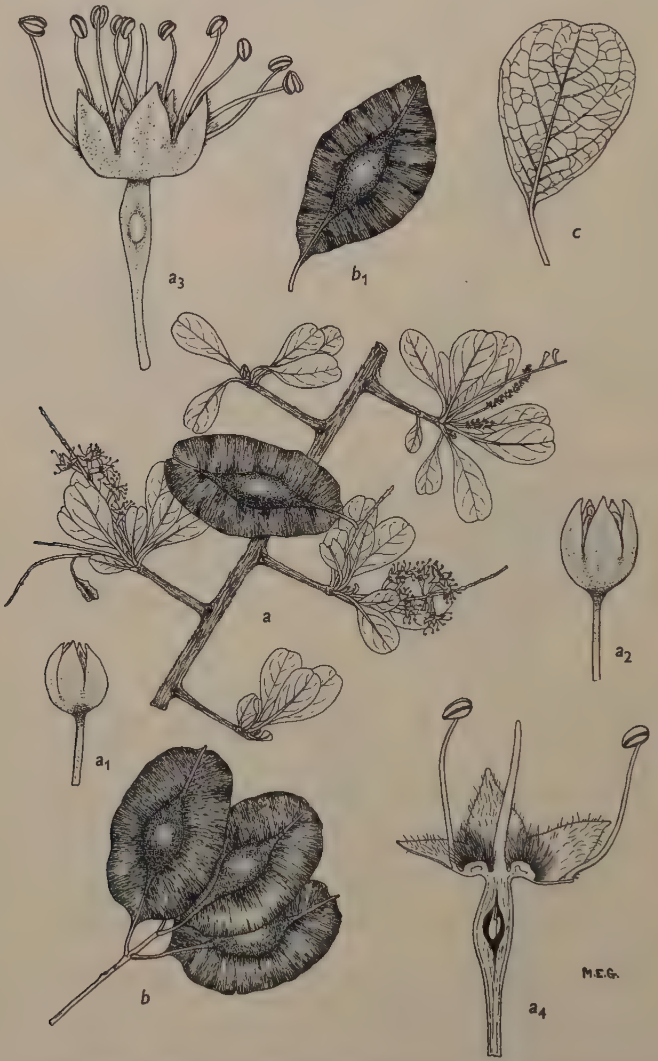


Fig. 3. *T. prunioides* Laws. *a*, from *Crooke* M206; a_1–a_4, from *Morze* 138; *b*, from *Lovemore* 21; b_1, *c*, from *Martin* 540.

Variation in this species is dealt with under the heading 'taxonomic history'. Fig. 3 illustrates the range of leaf-shape and size.

Since the above was written, several gatherings of this species from the coastal parts of Kenya (*Greenway & Rawlins* 8929, *Rawlins* 332, 333, 334) and Tanganyika (*Semsei* 2078, 2081, 2088, 2112) have become available, in which the lateral shoots, instead of ceasing growth after a few years and remaining at right-angles to the main stem, seem to grow indefinitely at a slow rate and curve upwards, so that they cease to be inserted at right-angles (F.W.).

KENYA. Lamu Dist., Manda Island nr. Lamu, frt., Sept. 1937, *Mohammed Abdulla* 3850 (EA, K), spreading tree 10 m. high, common along coast, especially on saline soil. Digo Dist., Mwachi, nr. Mombasa, fl., frt., Sept. 1936, *Dale* 1047 (EA, FHO), small tree or shrub 10 m. high. Kitui Dist., Kitui Hills, alt. 1000 m., frt., Jan. 1937, *Gardner* 3600 (EA, K). Northern Frontier Dist., Dandu, alt. 830 m., fl., Apr. 1952, *Gillett* 12779 (K), on red sandy loam, frequent tree 8 m. high with grey bark exfoliating in thick, narrow, vertical pieces, fls. white. Teita Dist., 8 km. N.W. of Tsavo R. on Mombasa Rd., alt. 670 m., frt., Jan. 1952, *Trapnell* 2223 (FHO, K), erect, rigid shrub or small tree; on eroded orange-coloured sandy loam with thick bed of limestone concretions.

TANGANYIKA TERRITORY. Lushoto Dist., Mnazi, alt. 600 m., frt., May 1939, *Gillman* 779 (EA, K), tree 4–5 m. high. Korogwe Dist., Kamba, alt. 500 m., fls., frt., Jan. 1930, *Greenway* 2047 (EA, FHO, K), scattered but fairly common tree in *Acacia*, desert-grass country; much-branched tree 10 m. high with green fls. and bright scarlet frt. Pare Dist., Gonja-Ndungu, alt. 100 m., frt., Feb. 1930, *Greenway* 2118 (EA, FHO, K), in *Acacia*, desert-grass formation; much-branched tree 10 m. high with purple frt. Lushoto Dist., W. Usambaras, Mkomazi, alt. 500 m., frt., Apr. 1934, *Greenway* 3936 (EA, FHO, K), occasional in *Acacia*, desert-grass formation, much-branched tree up to 10 m. high with rounded crown and dark plum-coloured frt. Usambaras, frt., Mar. 1893, *Holst* 2381 (K, isotype of *T. holstii*).

PORTUGUESE EAST AFRICA. Boroma Dist., Msusa, on summit of rocky hill 1 km. from Zambezi R., alt. 340 m., frt., July 1950, *Chase* 2696 (FHO), tree 7 m. high with scarlet frt. Makanga Dist., Tete, fl., Dec. 1858, *Kirk* s.n. (K, syntype); frt., Feb. 1859, *Kirk* s.n. (K, lectotype). Moatize, frt., May 1948, *Mendonça* 4107 (BM, K), tree 10–12 m. high, in deciduous forest. Boroma Dist., Boroma, fl., frt., 1891, *Menyhart* 766a (K). Guija Dist., Limpopo R., between Guija and Caniçado, frt., May 1944, *Torre* 6556 (BM, K), tree 6–10 m. high, in open deciduous forest.

S. RHODESIA. Wankie Dist., Victoria Falls, fl., 1904, *Allen* 122 (K), tree 7–8 m. high. ?Mtoko Dist., Nyanyadzi Settlement, Muwushu Reserve, fl., frt., Oct. 1950, *Crook* M206 (FHO), in tree veld; very common tree up to 15 m. high, with cream fls., and wine-coloured frt. Mtoko Dist., Mtoko Reserve, frt., Apr. 1951, *Lovemore* 21 (FHO), on sandy soil nr. Mazoe R.; tree 10 m. high, bark grey, rough, fluted, slash yellow. Chipinga Dist., Sabi R., nr. Birchenough Bridge, fl., Oct. 1946, *McGregor* 51/46 (FHO), tree 5 m. high, in tree veld. Gwanda Dist., about 80 km. N. of Beit Bridge towards Gwanda, frt., May 1948, *Rodin* 4515 (K), bush 3 m. high, with fragrant white fls. and reddish frt.

N. RHODESIA. Livingstone Dist., Sala R., about 19 km. S. of Bombwe, frt., Feb. 1933, *Martin* 540 (FHO, K), in mopane woodland. Id., Katombora, fl., Jan. 1948, *Morze* 138 (FHO), tree 5 m. high, on edge of low 'lupane' woodland. Mazabuka Dist., Gwembe, alt. 500 m., frt., Mar. 1934, *Trapnell* 1465 (K), small tree 5–8 m. high, on basic clay soils. Id., Gwembe Valley, about 1 km. S. of Mambo's village, frt., Mar. 1952, *White* 2357 (FHO), in open *Sclerocarya caffra*, *Adansonia*, *Combretum imberbe*, *Colophospermum mopane* woodland on shallow alluvium overlying Karoo mudstone.

BECHUANALAND PROTECTORATE. Batawana Reserve, Maun Camp on bank of Thamalakan R., frt., June 1937, *Erens* 321 (K), tree 8–10 m. high. Kwebe Hills, about 32 km. S. of Lake Ngami, alt. 1000–1200 m., fl., frt., 1897, *Lugard* 41 (K), tree 7–10 m. high, 0·75 m. girth, with white fls. and dark red frt. Bamangwato Reserve, nr. Kasinka, frt., *O. B. Miller* B 190 (FHO), in *Combretum* thicket marginal to *Baikiaea* forest, spiny tree to 10 m. high. Francistown, fl., frt., Jan. 1926, *Rand* 33 (BM), small tree, fls. strongly scented in evening. Bangwaketsi-Bakwena Reserves, kopjes between Mabele and Pudi, frt., May 1930, *G. van Son* 28818 (BM, K).

ANGOLA. Huila Dist., nr. Namacunde and Vila Pereira d'Eça, frt., 1937, *Miss Powell-Cotton* 1084 (BM), tree in sandy flat country. Benguela Dist., Benguela, frt., June 1859, *Welwitsch* 4290, 4344 (BM, syntypes of *T. benguellensis*), in bushy places nr. the coast. Mossamedes Dist., Boca do Rio Bero, on sea coast, frt., July 1859, *Welwitsch* 4291, 4337 (BM, syntypes of *T. benguellensis* var. *ovalis*), in sandy thickets nr. the town. Huila Dist., between Lopolo and Nene, frt., Feb. 1860, *Welwitsch* 4292 (BM, syntype of *T. benguellensis* var. *ovalis*), in bushy, hilly, rather dry places.

SOUTH WEST AFRICA. Grootfontein Dist., Grootfontein, frt., Jan. 1909, *Dinter* 920 (BM). Karibib Dist., Karibib, Kalkberge, frt., Jan. 1934, *Dinter* 6900 (BM, K). Omaruru Dist., Namib Desert, Spetzkoppe, alt. 1200 m., fl., frt., Apr. 1950, *Macdonald* 566 (BM), tree 5 m. high with white fls., on banks of water courses. Karibib Dist., Usakos, alt. 800 m., frt., May 1886, *Marloth* 1263 (OXF), tree 4 m. high. Ovamboland Reserve, Olukonda, fl., Mar. 1886, *Schinz* 433 (K, isotype of *T. rautanenii*).

TRANSVAAL. Zoutpansberg Dist., Louis Trichardt, between Messina and Dongola Reserve, frt., Jan. 1949, *Codd* 5488 (K). Letaba Dist., 26 km. S. of Letaba Camp, in low veld on stony slopes nr. Olifants R., alt. 300 m., fl., Nov. 1946, *Codd & Dyer* 4686 (K), common shrub 3 m. high with drooping branches and white fls. Pietersburg Dist., 80 km. N. of Gravelotte Station, st., Aug. 1934, *Galpin* 13531 (K), occasional tree 5 m. high with pinkish purple frt. Zoutpansberg Dist., Messina, fl., Nov. 1916, *Pole Evans* H 13101 (K). Pilgrims Rest Dist., Sabie, fl., Nov. 1917, *Pole Evans* H 16920 (K).

Taxonomic history

The five synonyms described after *T. prunioides* differ for the most part only slightly in size of leaves and fruits, both from the latter species and from one another. The measurements given below are those found in the original descriptions. The type material on which *T. prunioides* and its synonyms are based is given in brackets.

T. prunioides (*Kirk* s.n.!, *Kirk* s.n.!) has lvs. 2·5–5 cm. long, frts. 5 × 4 cm.

T. porphyrocarpa (*Schinz* 419) and *T. rautanenii* (*Schinz* 433!), both from South West Africa, and described by the same author in the same publication, are scarcely differentiated on size of leaves and fruits. The former with lvs. 3 × 1·5 cm., frts. 3–5 × 1·3–2·3 cm.; the latter with lvs. 1·5–3 × 1·1–1·6 cm., frts. 4·5 × 2·5 cm. There is nothing in the shape of the leaves or the fruits to separate them. *T. porphyrocarpa* is reduced to a synonym of *T. prunioides* by Engler and Diels in their monograph.

T. holstii (*Holst* 2381!) from East Africa, has lvs. 5–7 × 3·5–4 cm., frts. 3–3·5 × 2–2·5 cm. The leaves are somewhat larger than those in any of the other 'species' and the fruits are different from those of the other type specimens in the deeply emarginate apex and truncate base.

T. petersii (*Peters* s.n.) from Portuguese East Africa (Tete, the type-locality of *T. prunioides*), has lvs. 2·5 × 1–1·5 cm., frt. *c.* 3·5 cm. long. It is also treated as a synonym of *T. prunioides* by Engler and Diels.

T. benguellensis (*Welwitsch* 4290!, 4334!) from Angola, has lvs. 2·5–5·75 × 1·3–3 cm., frts. 4·5–5 × 2–2·5 cm., and var. *ovalis* (*Welwitsch* 4291!, 4337!, 4292!) based on more ovate fruits, 3·8–4·5 × 2·5–2·8 cm.

It can be seen from the measurements given above that there is a considerable overlap in size of the leaves and the fruits.

The type material of all these species, except *T. porphyrocarpa* and *T. petersii*, has been examined; Engler and Diels treated both as synonyms of *T. prunioides* and their views are followed here. A careful examination of type material of the remaining species, supplemented by many other gatherings, has failed to reveal any differences in arrangement of lateral shoots, length of lateral and spur-shoots leaf-shape, details of nervation, venation, indumentum, etc., which can serve to maintain these species even at the subspecific level.

The fruits of the type material of *T. prunioides* and *T. holstii* have somewhat different shapes, but a study of a large amount of material collected in Tanganyika and South Tropical Africa shows that the shape of the fruits is not constant, and that there are all degrees of variation between these two extremes.

Distribution and ecology

A very widely distributed species extending from northern and eastern Kenya, through the eastern districts of Tanganyika to western Portuguese East Africa, and from there more or less distributed throughout Southern Rhodesia and the southern parts of Northern Rhodesia, as far south as the north-eastern Transvaal, and extending westwards to Bechuanaland, northern South West Africa, and to the western parts of southern Angola.

In Kenya it occurs in the *Acacia*, desert–grass savannah region, and according to Dale (8) it is a common constituent of the lowland evergreen edaphic forest of a palm-stand type, which occurs east of the Tana River. It also occurs in the coastal savannah with patches of evergreen forest and scrub, and is common in the scrub forest on the lower northern slopes of the Shimba Hills. It is a common species in the dense bush country from Samburu to Mackinnon Road, and probably also between Gongoni and the Tana River.

Over most of its range it is of frequent occurrence in the hotter and drier low-lying areas, especially in the larger river valleys. Several authors and collectors record it as being associated with *Colophospermum mopane* and over much of its range the two species occur together.

In the Transvaal (7) it occurs in the low veld types of savannah, and shows a distinct preference for drier situations occupied by such types as *mopane*, which occupies practically all the northern parts of the Kruger National Park, and Red Bush-Willow (*Combretum apiculatum*), which stretches along the western border of the Park to the Olifants River. In the southern parts of the Park it occurs along dry water courses. It is noticeably absent from around Pretorius Kop, where the rainfall is more than 750 mm. (30 in.). It is a common species in the low country north of Zoutpansberg, and also occurs in the broad-leaved savannah around Pietersburg.

In Bechuanaland it is found in the *mukusi* (*Baikiaea plurijuga*) region and in *mopane* woodland, and extends southwards into the much drier region of *Acacia* scrub. It is common (31) in the flat grassy plain between Rakops and Maun, and in the Kalahari thorn scrub south of Lake Ngami; it also occurs as isolated trees, with *T. sericea* and *Grewia* sp., on the flanks of the rocky hills south-west of the lake.

In South West Africa it occurs in the *mopane* woodland of the north, and in the *Acacia* scrub south of Grootfontein. *Walter* (37) provides an interesting account of its distribution and ecology. In the north-east it is often gregarious and occurs on well-drained soils. From there, it extends, becoming rarer, towards the west almost as far as the Namib desert, but in these drier regions, where the rainfall may scarcely exceed 100 mm. (4 in.) per annum it becomes increasingly dependent on access to supplies of ground water.

In Angola (16) it is common in *miombo* woodland regions in Cuanza, Benguela and Huila districts, and occurs on granite rocks near the coast at about 600 m. alt. at Catengue in Mossamedes Dist. In the latter district it also occurs in desert scrub vegetation between Pedra Grande and Serra de Lua at 70–600 m. alt. and is one of the dominant species near Pica do Azevedo. It also occurs in fringing forest along Muve River. In Benguela Dist. it is found in *Acacia* scrub between Hanha and Quilenges.

(4) **T. brevipes** Pampan., *Bull. Soc. Bot. Ital.* p. 16 (1915); Chiov., *Result. Sci. Miss. Stefan.-Paoli Som. Ital.* 1, 211 (1916).

See Fig. 4. Small tree, 7–10 m. high, with thorny rough bark; bark of branchlets fibrous, light brown to greyish brown. Long shoots straight, with irregularly arranged lateral shoots diverging at obtuse angle. Lateral shoots ending in a spine and bearing 1–3 lateral spur-shoots 0·3–0·5 cm. long. Many spur-shoots also borne directly on long shoot. Spines occasionally present on long shoots, 1–2 cm. long. *Lvs.* narrowly or broadly obovate to broadly oblanceolate, apex obtuse to rounded, sometimes emarginate, base acute to cuneate, 3 × 1·3–5 × 3·5 cm., glabrous or sparsely pubescent beneath, chartaceous; *upper surface*: midrib and secondary nerves ± impressed, tertiary nerves and venation scarcely visible; *lower surface*: midrib subprominent, secondary nerves slightly raised, tertiary nerves visible but not or scarcely raised, venation scarcely visible; petiole 0·6–0·7(–1) cm. long. *Infl.* 6–7·5 cm. long, peduncle 1·5–3 cm. long, very sparsely pilose; *fl.* glabrous; calyx-lobes acute. *Frt.* suborbicular, apex rounded, with

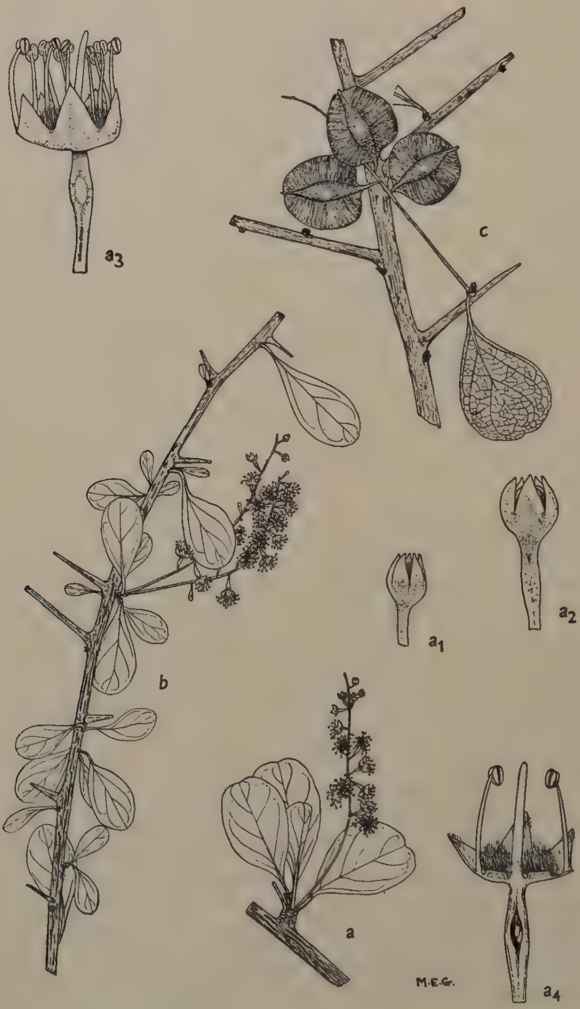


Fig. 4. *T. brevipes* Pampan. *a*, a_1–a_4, from *Scasselatti* 119; *b*, from *Bally* 5866; *c* from *Paoli* 1339.

style persistent, base rounded, 1·8 × 1·9–2·4 × 2 cm., glabrous, yellowish brown; pedicel 0·1–0·2 cm. long.

All the available material is cited below and consists of flowering or sterile specimens and one fruiting specimen. This small amount of material shows only slight variation in leaf-size; the Somaliland specimens have rather larger leaves than those from Kenya—see Fig. 4.

ETHIOPIA. Aisaita, on flooded banks of R. Hawash, 450 m. alt., fl. May 1957, *Hemming* 1230 (K).

ITALIAN SOMALILAND. Uebi Scebeli, between Muccoidère and Balaad, frt., Nov. 1913, *Paoli* 1339 (FI, lectotype). Webi, st., July–Aug. 1891, *Robecchi Brichetti* 244 (FI). Arrar, fl., 1912, *Scassellati* 18 (FI, paratype); st., *Scassellati* 12 (FI, paratype). Uebi Gof, Giuba Valley, fl., 1912, *Scassellati* 119 (FI), paratype).

KENYA. Tana R. Dist., Garissa, in riverine bush along Tana R., alt. 133 m., fl., Sept. 1948, *Bally* 5866 (K), scrambling bushy tree 7 m. high with white fls. Id., nr. Tana R. at Kau, fl., Oct. 1936, *Dale* 3525 (EA, FHO, K), tree up to 10 m. high with rough, thorny bark and white fls.

Distribution and ecology

Nothing appears to have been published about the distribution or ecology of this species. One collector has recorded its occurrence in a riverine bush type of vegetation; it is distributed from Central Italian Somaliland to as far south as the Tana River in Kenya, and so seems to be confined to the *Acacia*–desert-grass savannah regions with an erratic annual rainfall of about 250 mm. (10 in.).

(5) **T. parvula** Pampan., *Bull. Soc. Bot. Ital.* p. 17 (1915); Chiov., *Fl. Somala*, **2**, 207 (1932).

See Fig. 5. Shrub or small tree, 3–5 m. high; bark of bole striated, blackish; bark of branchlets finely striated, whitish grey. Long shoots straight, with irregularly arranged lateral shoots diverging at obtuse angle. Lateral shoots ending in a spur-shoot, rarely in a spine, and bearing 10–15 or more lateral spur-shoots 0·2–0·3 cm. long. Numerous spur-shoots also borne directly on long shoot. *Lvs.* obovate or spathulate, apex rounded, emarginate, base cuneate, 0·5 × 0·3–1 × 0·4 cm., glabrous or almost so, chartaceous, pale green, nerves inconspicuous on both surfaces; petiole 0·2 cm. long. *Infl.* 1·2–1·5 cm. long, peduncle 0·6 cm. long, glabrous; *fl.* glabrous; calyx-lobes acute. *Frt.* ovate-elliptic, apex rounded, emarginate, base cuneate to subtruncate, 1·8 × 1·2–2 × 1·4 cm., glabrous, reddish; pedicel 0·2–0·5 cm. long.

As in the case of *T. orbicularis* and *T. brevipes*, *T. parvula* is not very well known. The leaves are not very variable in shape, and only show slight differences in size.

ITALIAN and BRITISH SOMALILAND. Chisimaio, Lake Dera, st., 1926, *Balladelli* 267 (FI). English bank of Giuba R., between Revai and Sorori, st., July 1913, *Paoli* 497 (FI, paratype). In woodlands between Bardera and Mansur, frt., July 1913, *Paoli* 580 (FI, lectotype). Nr Lugh, fl., Oct. 1913, *Paoli* 992a, 992b (FI, paratypes).

KENYA. Northern Frontier Dist., at base of Eillass, alt. 500 m., frt., Jan. 1949, *Dale* 741 (EA, K), single-stemmed tree 5 m. high, 0·1 m. girth, with striated, black bark. Kitui Dist., Sosome to Kindelongwe, fl., Dec. 1952, *Edwards* 212 (EA). Northern Frontier Dist., Dandu, alt. 870 m., frt., Mar. 1952, fl., May 1952, *Gillett* 12588 (FHO, K), on gravelly eroded soil at foot of mountain; small tree 3 m. high, with very small leaves, cream fls. and reddish frt.; several trees in one area only.

Distribution and Ecology

Nothing has been published about its distribution or ecology. Its distribution in Kenya comes well within the desert scrub and *Acacia*, desert–grass savannah regions of the north and east. It extends into southern Italian Somaliland, where it occupies a similar type of vegetation.

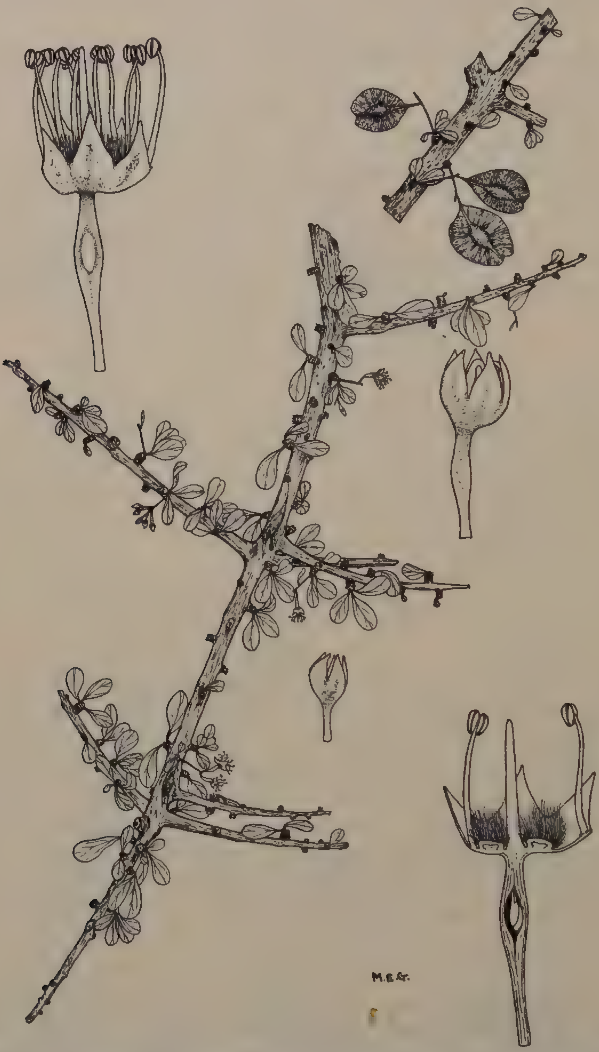


Fig. 5. *T. parvula* Pampan. Flowering specimen from *Gillett* 12588. Fruiting specimen from *Dale* 741.

(6) **T. spinosa** Engl., *Pflanzenw. Ost-Afr.* C, 294 (1895); Engl. & Diels, *Monogr.* **4**, 22, t. 13B (1900); Engl., *Jahrb.* **28**, 441 (1901); Engl., *Jahrb.* **39**, 515 (1907); Engl., *Pflanzenw. Afr.* **3** (**2**), 725 (1921); Chiov., *Fl. Somala*, **2**, 207 (1932); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr), **2**, 146 (1949); Eggeling, *Indigenous Trees Uganda Prot.* ed. 1, 47 (1940), ed. 2, 93 (1951).

See Fig. 6. Small tree, 5–20 m. high, with straight trunk, flat crown and horizontal branches; bark of bole longitudinally fissured, grey; bark of branchlets greyish brown or pale whitish grey. Long shoots zigzag, with irregularly arranged lateral shoots diverging at obtuse angle. Lateral shoots ending in a spur-shoot and with or without 1–2 lateral spur-shoots 0·7–1·5 cm. long. Spur-shoots also occasionally borne directly on long shoot. Spines frequently present, 0·5–1·5 cm. long, 2–3 diverging from same point, occurring at base of spur-shoots. *Lvs.* broadly obovate, apex rounded to subtruncate, deeply emarginate, base sharply cuneate, 1·8 × 1–3 × 2 cm., glabrous or very sparsely pubescent, chartaceous, main nerves raised and equally conspicuous on both surfaces, venation inconspicuous; petiole 0·3–0·5 cm. long. *Infl.* 5–6 cm. long, peduncle 1–1·2 cm. long, sparsely to densely pubescent; *fl.* glabrous; calyx-lobes acute. *Frt.* oblong-elliptic, apex rounded to subtruncate, emarginate, base subtruncate, 2 × 1–2·5 × 1·2 cm., glabrous, reddish purple; pedicel 0·3 cm. long.

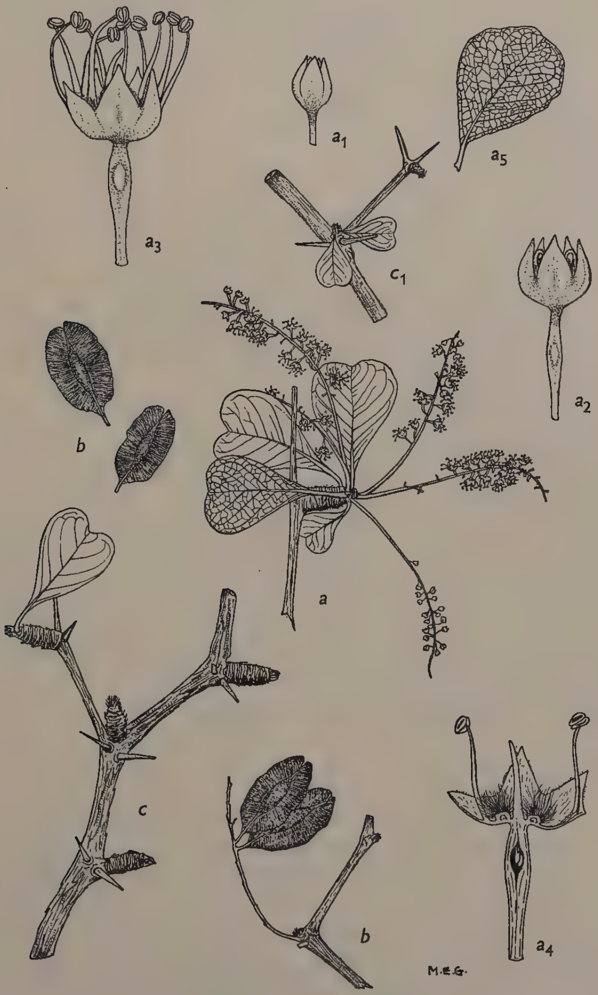


Fig. 6. *T. spinosa* Engl. *a*, a_1–a_5, from *Elliot* 1374; *b*, from *Greenway* 4210; *c*, from *Vaughan* 2414; c_1 from *Greenway* 5814.

The leaf-shape in *T. spinosa* is remarkably constant; leaf-size, however, varies considerably, as shown in Fig. 6. The smaller-leaved form occurs mainly towards the northern edge of its distribution in Italian Somaliland and the Sudan Republic, and in its more coastal habitats in Tanganyika. The fruits remain fairly constant in shape and size over its entire range.

ITALIAN SOMALILAND. 40 km. S. of Bulo Burti, st., Oct. 1951, *Bond & Pechanec* 34 (EA). Gharabursin, nr. Obbia, frt., *Drake-Brockman* 953 (K). 43 km. S. of Belet Wein, alt. 200 m., st., Nov. 1952, *Hemming* 120 (EA, K) thorny tree up to 4 m. high; in mixed woodland with *Acacia tortilis* and *Ziziphus* sp.

SUDAN REPUBLIC. Equatoria Prov., Torit, frt., Mar. 1948, *Jackson* 198 (SGH). Id., Ikotos, alt. 300 m., fl., Feb. 1949, *Jackson* 625 (FHO), in dry savannah on sandy soil, at present cultivated; tree 10 m. high, trunk erect with branches extending horizontally, bark scaling in longitudinal strips, fls. white. Id., Lauru, S.W. of Kapoeta, Didinga Mts., frt., Sept. 1940, *Myers* 13465 (K), frequent small tree in grassland, branches horizontal, trunk longitudinally fissured, dark brown. Id., Kapoeta, st., *Sgt. Stanley* s.n. (SGH).

UGANDA. Karamoja Dist., between Amudat and Lorengidwat, frt., Feb. 1936, *Eggeling* 2793 (K), in deciduous scrub-savannah, spinous tree or large bush to 6 m. high with small, dark brown frt. Id., Kanyanganeng, W. Suk, fl., Feb. 1936, *Eggeling* 2978 (K), tree 8 m. high, branches in whorls giving storeyed appearance, spines paired, straight, sharp. Id., Kakumongole, Akwamunyeng, alt. 1300 m., frt., Jan. 1937, *Thomas* 2200 (K), in dry forest, tree 17 m. high with horizontal branches. Id., Upe country, frt., Feb. 1954, *Wilson* H61/54 (EA), tree in eroded gulley.

KENYA. Northern Frontier Dist., Ijara to Chongoli, alt. 80 m., st., Jan. 1943, *Bally* 2095 (K), tree with straight bole. Baringo Dist., Kamasia Hills, st., July 1953, *Bally* 9031 (K), on rocky ground, characteristic tree of this area, 10 m. high with very straight trunk. Digo Dist., Mwachi, nr. Mombasa, fl., *Elliot* 1374 (FHO, K), in open grassland or bush but not in forest; tall tree of coast district with horizontal branches in whorls. Kilifi Dist., Marereni, about 26 km. N. of Mambrui, fl., frt., *Graham* 230 a, 230 b (BM, EA, FHO, K), tall deciduous tree with slightly scented, white fls. Digo Dist., Mombasa, frt., Nov. 1884, *Wakefield* s.n. (K, syntype).

TANGANYIKA TERRITORY. Morogoro Dist., Kissaki Steppe, frt., Nov. 1898, *Goetze* 47 (K, lectotype). Tanga Dist., Mtimbwani, alt. 16 m., frt., Dec. 1935, *Greenway* 4210 (EA, FHO, K), on dark brown soil overlying a red earth, in open *Terminalia–Sclerocarya–Acacia* association, tree up to 20 m. high with horizontal branches and flat crown, bark fissured, black. Morogoro Dist., between Morogoro and Turiani, on Morogoro–Korogwe Rd., alt. 650 m., fl., Oct. 1938, *Greenway* 5814 (EA, FHO, K), locally common on grey sandy loam in *Acacia nigrescens–Acacia* spp. woodland, much-branched spiny tree up to 12 m. high with horizontal branches, bark rough, grey, fls. white, frt. small, red. Moshi Dist., Moshi–Himo Rd., frt., Nov. 1951, *Hughes* 148 (EA, FHO), in open savannah woodland, tree 5 m. high, 0·25 m. diam. Kisarawe Dist., nr. Kunduchi, fl., Oct. 1936, *Vaughan* 2414 (BM, FHO), large flat-topped tree with white fls.

Distribution and Ecology

T. spinosa is distributed more or less throughout the central region of East Tropical Africa, occupying southern Italian Somaliland, the southern parts of the Equatoria Province of the Sudan Republic, the eastern districts of Uganda, the Northern Frontier and coastal districts of Kenya, and penetrates as far south as north-eastern Tanganyika; it extends through the coastal districts of the latter territory to as far as Kunduchi. Most of its range is well within the *Acacia*, desert–grass savannah region; in Kenya and Tanganyika it also occurs in the coastal savannah, which contains patches of evergreen forest, thicket and scrub.

In the Karamoja District of Uganda (36) it is common in the *Acacia* woodland and thicket in the east, and this extends in a wide belt south from Moroto and east from Kadam to the south-east corner of the district.

(7) **T. randii** Bak. f., *J. Bot., Lond.*, **37**, 435 (1899); Engl., *Jahrb.* **39**, 515 (1907); Fries, *Wiss. Ergebn. Schwed. Rhod.-Kongo Exped.* 1911–12, **1**, 175 (1914); Engl., *Pflanzenw. Afr.* **3** (**2**), 725 (1921); Pole Evans, *Bot. Surv. S. Afr., Mem.* **21**, 31 (1948).

See Fig. 7. Shrub, 1–2 m. high, or small bushy tree, 3–12 m. high, with rounded crown; bark of bole longitudinally fissured, dark brown; bark of branchlets grey to brown. Long shoots zigzag, with irregularly arranged lateral shoots diverging at obtuse angle. Lateral shoots ending in a spur-shoot and with or without 1–2 lateral spur-shoots 0·4–1 cm. long. Spur shoots also occasionally borne directly on long shoot. Spines frequently present, 0·6–1·4 cm. long, solitary or 2–3 diverging from same point, occurring at base of spur-shoots. *Lvs.* narrowly to broadly oblanceolate, apex obtuse to rounded, mucronate or slightly emarginate, base cuneate, 1 × 0·7–2·5 × 1·2 cm., sparsely sericeous-pubescent becoming glabrous, chartaceous, pale green to slightly glaucous, nerves inconspicuous on both surfaces; petiole 0·6–1·4 cm. long. *Infl.* 3–3·5 cm. long, peduncle 1·5 cm. long,

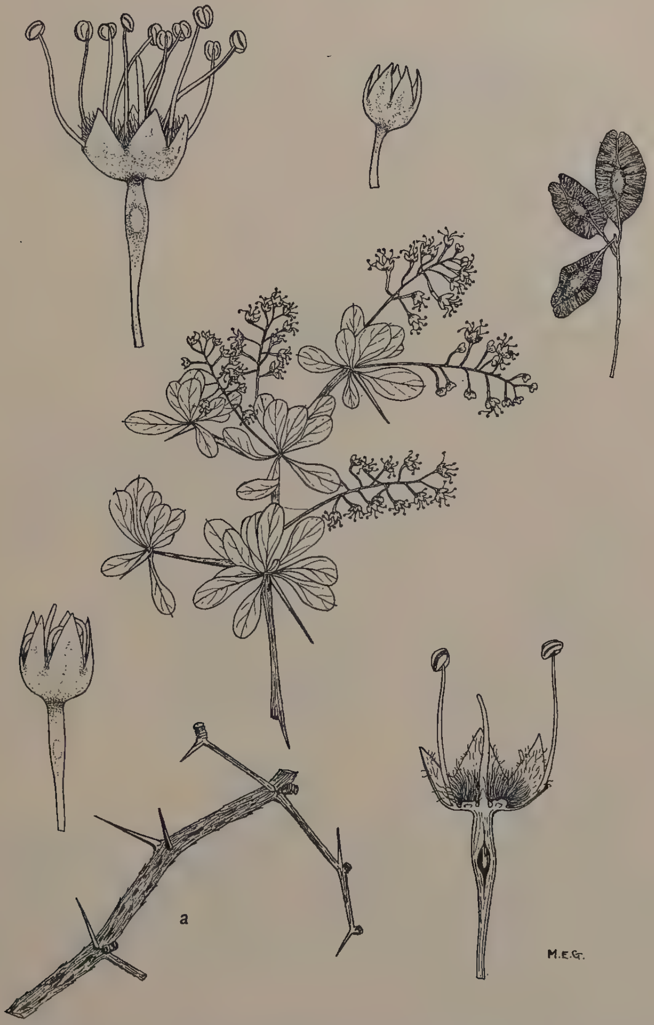


Fig. 7. *T. randii* Bak. f. Flowering specimen from *Angus* 1127. Fruiting specimen from *Keay* FHI 21312. *a*, from *White* 2227.

glabrous; *fl.* glabrous; calyx-lobes subacute. *Frt.* elliptic to oblong, apex obtuse, deeply emarginate, base acute to subtruncate, 1·5 × 1–2·5 × 1·2 cm., glabrous, purplish red to purplish yellow; pedicel 0·5–0·7 cm. long.

T. randii shows very little variation other than that given in the above description. The leaves, and also the fruits, retain essentially the same shape over its entire range, with only minor differences in size. The most conspicuous difference in the leaves is shown by the Bechuanaland material where the leaves are much smaller and narrower.

PORTUGUESE EAST AFRICA. No locality given, fl., Nov., *Allen* 63 (K), thorny shrub with cream fls.

SOUTHERN RHODESIA. Salisbury Dist., Beatrice, alt. 1400 m., frt., Sept. 1923, *Eyles* 4527 (K), small tree with straight bole. Wankie Dist., Victoria Falls, frt., 1911, *Fries* 100 (K). Bubi Dist., Bakumbusi, about 80 km. N. of Bulawayo, in Dromoland Estate, frt., June 1947, *Keay* FHI 21312 (FHO), with *Colophospermum mopane*, frequent in clumps of woodland on mounds between streams and *Terminalia sericea* zone, tree 12 m. high, bark of bole fissured, dark brown, young frt. pink. Charter Dist., 24 km. N. of Enkeldoorn on Salisbury Rd., fl., May 1951, *Mylne* 23/51 (FHO), tree about 4 m. high. Bulawayo Dist., Bulawayo, fl., May 1898, *Rand* 325 (BM, holotype).

NORTHERN RHODESIA. Livingstone Dist., below Victoria Falls, fl., Jan. 1953, *Angus* 1127 (FHO), on basaltic soils in open woodland on top of cliffs, with *Dirichletia*, *Croton* sp., *Colophospermum mopane*, *Acacia nigrescens* and *Kirkia acuminata*; small tree with rounded crown and abundant, showy, white fls. Id., Ngwesi Flats, about 82 km. N.E. of Livingstone, frt., Mar. 1933, *Martin* 650 (FHO), on (?) basalt outcrop; bush to small tree 3 m. high. Id., on road to Livingstone, within 5 km. of Victoria Falls, frt., May 1948, *Rodin* 4495 (K), tree 7 m. high, spines up to 3 cm. long. Mazabuka Dist., Gwembe, alt. 500 m. fl., Mar. 1934, *Trapnell* 1471 (K), on calcareous nodular soils and gravels, by stream-sides, small tree 5 m. high. Livingstone Dist., Victoria Falls Reserve, frt., Mar. 1952, *White* 2227 (FHO), with *Combretum apiculatum*, *Diospyros quilöensis*, *Vitex* sp., *Grewia bicolor*, on very shallow clay soil overlying Karroo Basalt.

BECHUANALAND PROTECTORATE. Tati Concession, Tsessebe, st., Apr. 1931, *Pole Evans* 3244 (42) (K). Bamangwato Reserve, between Tutumi and Bushman Mine, frt., Apr. 1931, *Pole Evans* 3265 (13) (K). Kazungula, frt., Apr. 1936, *O. B. Miller* B 127 (BM, FHO), marginal to *mukusi* forest, shrub to 3 m. high. Unlocalized, 16 km. S. of Nakaneng, frt., June 1946, *O.B. Miller* B 429 (FHO), shrub 1·5 m. high in 'island' of dense woodland surrounded by open savannah.

Distribution and ecology

T. randii is confined to South Tropical Africa, occurring in the *miombo* and *mopane* woodland areas of Mazabuka and Livingstone districts of Northern Rhodesia, extending southwards into the *mukusi* forest region in northern Bechuanaland, and occurs in *mopane* woodland to just beyond the Makarikari Pan; it is particularly common in the western half of Southern Rhodesia, where it occurs mainly in *mopane* woodland, but also in the outliers of fine-leaved savannah woodland around Bulawayo, in which *Acacia* spp. and *Commiphora* spp. predominate.

(8) **T. stuhlmannii** Engl., *Pflanzenw. Ost.-Afr.* C, 294 (1895); Engl. & Diels, *Monogr.* **4**, 22, t. 10 A (1900); Engl., *Jahrb.* **28**, 441 (1901); Fries, *Wiss. Ergebn. Schwed. Rhod.-Kongo Exped.* 1911–12, **1**, 175 (1914); Engl., *Pflanzenw. Afr.* **3** (2), 725 (1921); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr.), 2, 146 (1949); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, **2**, 149 (1954).

See Fig. 8. Shrub or small tree, 3–12 m. high, with flattened crown and horizontal branches; bark of bole with fine longitudinal fissures, brownish grey or whitish grey; bark of branchlets grey or greyish brown. Long shoots zigzag, with irregularly arranged lateral shoots diverging at obtuse angle. Lateral shoots ending in a spur-shoot ± 1·2 cm. long and rarely bearing lateral spur-shoots. Spur-shoots also occasionally borne directly on long shoot. Spines occasionally present, 0·7–1 cm. long, solitary or 2 diverging from same point, occurring at base of spur shoots. *Lvs.* narrowly or broadly oblanceolate, occasionally obovate, apex obtuse to rounded, slightly emarginate or mucronate, base acute to subobtuse 1·5 × 1–6 × 2 cm., glabrous, margin recurved, chartaceous, glaucous-green above with pale green midrib, pale yellowish green beneath; *upper surface*: midrib impressed, secondary nerves raised, tertiary nerves and venation scarcely visible; *lower surface*: midrib subprominent, secondary and tertiary nerves and venation conspicuous but not raised; petiole 0·2–0·4 cm. long. *Infl.* 6–7·5 cm. long, peduncle 2·5–3 cm. long, glabrous; *fl.* glabrous; calyx-lobes acuminate or apiculate. *Frt.* elliptic-oblong, apex obtuse, deeply emarginate or entire, base obtuse to truncate and slightly decurrent,

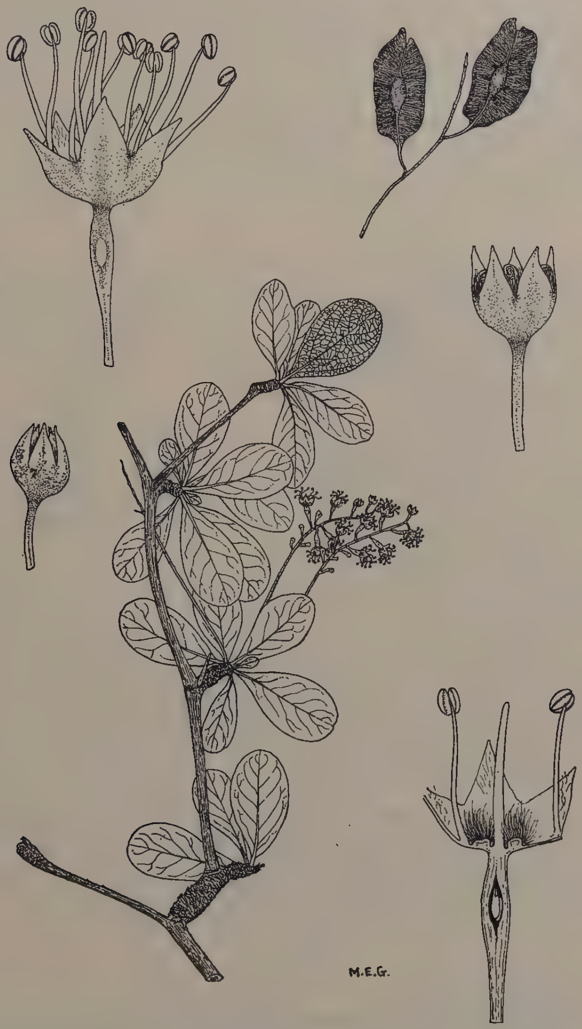


Fig. 8. *T. stuhlmannii* Engl. Flowering specimen from *Angus* 1118. Fruiting specimen from *Angus* 1123.

2·5 × 1·5–3 × 1·8 cm., glabrous, purplish yellow to purplish red; pedicel 0·5–0·7 cm. long.

On the whole the leaves of *T. stuhlmannii* remain fairly constant in shape, that is, essentially oblanceolate; although varying in length, they are rarely more than 2 cm. broad. The fruits remain fairly constant in shape and size.

TANGANYIKA TERRITORY. Kondoa Dist., nr. Hundwi, fl., Jan. 1928, *Burtt* 1074 (BM, FHO, K). Shinyanga Dist., Shinyanga, fl., Feb. 1935, *Burtt* 5077 (BM, K), in thickets on 'hard-pan' soils among *Commiphora schimperi* and *C. subsessilifolia*; small flat-crowned tree, bark smooth, dark brown, wood very hard, termite resistant. Iringa or Njombe Dist., Uhehe tribal area, Mloha R., alt. 900 m., fl., Jan. 1899, *Goetze* 493 (K). Mpwapwa Dist., Mpwapwa, fl., frt., Feb. 1930, *Hornby* 167 (EA, FHO, K), on hill slopes, tree 6 m. high. Iringa Dist., Nyangolo, 58 km. N. of Iringa on Dodoma Rd., top of Ruaha escarpment, alt. 1500 m., fl., Jan. 1952, *Wigg* 987 (EA, FHO, K), small tree with spreading crown.

PORTUGUESE EAST AFRICA. Boroma Dist., Boroma, frt., Dec. 1891, *Menyhart* 766 (K, lectotype).

SOUTHERN RHODESIA. Sebungwe Dist., Kariyangwe, fl., Dec. 1951, *Lovemore* 229 (FHO), on sandy soil with *Colophospermum mopane* and *Commiphora* spp., spreading tree 7 m. high with smooth, grey bole. Wankie Dist., Victoria Falls, fl., Dec. 1930, *Pardy* 4757 (BM, FHO). Darwin Dist., Darwin, at foot of Zambezi Valley escarpment, frt., June 1923, *Swynnerton* 4042 (K). Hartley Dist., Gatooma, alt. 1300 m., st., Apr. 1927, no collector's name given 4922 (FHO).

NORTHERN RHODESIA. Livingstone Dist., nr. Livingstone, fl., frt., Jan. 1953, *Angus* 1118 (FHO), on alluvium in open woodland fringing Zambezi R., with *Colophospermum mopane, Acacia nigrescens, Piliostigma, Allophylus, Securinega, Phyllanthus, Trichilia roka*; tree 7 m. high with sparse, flattened crown and leaning trunk 0·12 m. dbh; bark rough with fine longitudinal furrows, fls. white, frt. purple-pink. Id., below Victoria Falls, fl., frt., Jan. 1953, *Angus* 1123 (FHO), on basaltic soil in open woodland on top of cliffs, with *Dirichletia, Croton, Colophospermum mopane, Acacia nigrescens, Kirkia acuminata*; small, flat-topped tree to 7 m. high with white fls. and plum-coloured frt. Mazabuka Dist., on Malamba R., Guimbe, fl., Jan. 1930, *Browne* 53 (FHO). Lundazi Dist., Mbuzi to Kalusa on eastern scarp face of Luangwa Valley, alt. 800 m., frt., Aug. 1938, *Greenway & Trapnell* 5628 (EA, K), common with *Commiphora* spp. and *Euphorbia* sp. in *Colophospermum mopane* woodland on brown soil over Karroo mudstone; horizontally branched tree up to 8 m. high, bark rough, greyish white, branches sometimes spiny. Mpika Dist., Munyamazi R., Luangwa Valley, frt., Oct. 1933, *Michelmore* 617 (K), common in broken *mopane* country, small, flat-topped, spiny, deciduous tree.

BECHUANALAND PROTECTORATE. Kazungula, frt., 1936, *O. B. Miller* B118 (FHO), marginal to *mukusi* forest; shrub up to 3 m. high with pink frt.

Distribution and ecology

T. stuhlmannii occurs in *Acacia* woodland types in central and eastern Tanganyika extending into the *miombo* woodland region of south-east Tanganyika; it appears more widespread in South Tropical Africa occurring in *mopane* woodland of north-western Portuguese East Africa, and in most of the northern districts of Southern Rhodesia (in the *miombo* and *mopane* woodland areas) westwards to the Southern Province of Northern Rhodesia, extending to the north along the Luangwa Valley; it also occurs in woodland types marginal to *mukusi* forest in Northern Bechuanaland.

In Tanganyika (5) it is common in the *Acacia–Commiphora* thorn savannah of the Lake and Central Provinces, especially near Kazikazi in small thickets around termite mounds. It appears in most of the central and eastern districts of Tanganyika.

According to Phillips (29) it is locally abundant in the *Combretum*–other species savannah on alluvial soils in the Central Province of Tanganyika, and is one of the principal trees in the *Grewia–Pseudoprosopis–Bussea*–other species deciduous thicket occupying large areas of country around Manyoni, Itigi, Matabele and Kazikazi and, as small patches, in Kahama Dist. near Buhondo.

(9) **T. polycarpa** Engl. & Diels, *Monogr.* **4**, 24, t. 12 A (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 725 (1921); Chiov., *Fl. Somala*, **1**, 172 (1929), **2**, 207 (1932).

T. kelleri Engl. & Diels, *op. cit.* 24, t. 12 B; Engl., *op. cit.* 725; Chiov., *op. cit.* 172 (1929), synon. nov.

See Fig. 9. Small tree, 5–7 m. high; bark of branchlets fibrous, greyish brown to purplish grey. Long shoots zigzag, occasionally almost straight, with irregularly arranged lateral shoots diverging at obtuse angle. Lateral shoots ending in a spur-shoot and bearing 1–2 lateral spur-shoots 1·2 cm. long. Spur-shoots occasionally also borne directly

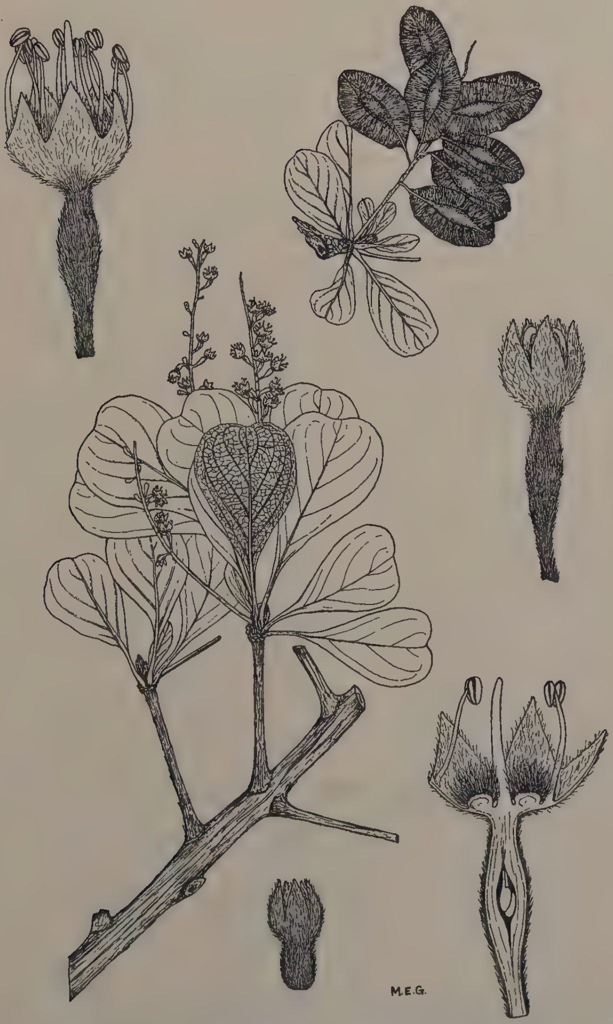


Fig. 9. *T. polycarpa* Engl. & Diels. Flowering specimen from *Keller* 222. Fruiting specimen from *Glover & Gilliland* 1191.

on long shoots. Spines absent. *Lvs.* obovate, apex rounded to truncate, broadly emarginate, base acute to cuneate, 3·5 × 1·8–5·5 × 3·2 cm., rather densely sericeous-pubescent beneath, more sparsely so above and becoming glabrous, chartaceous; *upper surface*: main nerves ± impressed, venation scarcely visible; *lower surface*: midrib prominent, secondary nerves subprominent, tertiary nerves and venation conspicuous but not raised; petiole, 0·7–1 cm. long. *Infl.* 7–9·5 cm. long, peduncle 2·5–3 cm. long, densely tomentose; *fl.*: lower receptacle densely tomentose, upper receptacle sparsely pubescent; calyx-lobes acute. *Frt.* elliptic-oblong, apex obtuse, emarginate, base obtuse to subtruncate, 2·5 × 1·2–3 × 1·5 cm., finely puberulous, yellowish purple; pedicel 0·3–0·4 cm. long.

T. polycarpa seems to be a very variable species, at least as far as the leaves are concerned; the two extremes in leaf size are shown in Fig. 9; there is a gradation between these which does not appear to have any connexion with their geographical or altitudinal distribution. The leaf-shape remains fairly constant. The fruits are also not very variable, either in shape or size.

ETHIOPIA. Ogaden, west of Shillave (Scillave), 44° 42′ E, 06° 25′ N, 400 m. alt., fl. Nov. 1955, locally common, *Ellis* 382 (K).

BRITISH SOMALILAND. Einad Al Hills, alt. 700 m., frt., Nov. 1929, *Collenette* 320 (K), in rather open position on northern slope of rocky hillside, tree 8 m. high with reddish frt. Eil Demet, alt. 1100 m., frt., Oct. 1932, *Gillett* 4321 (K), at edge of lava plateau, occasional tree 5 m. high with reddish frt. Ali Wein Mt., alt. 600 m., frt., Jan. 1933, *Gillett* 4828 (K), in open scrub in limestone ravine, small tree 4 m. high with reddish frt. Tug Gelakur along old oil road, frt., May 1945, *Glover & Gilliland* 1191 (FHO, K), tree 7 m. high, severely hacked about. Ainabo, alt. 1000 m., fl., Sept. 1941, *Capt. Peck* 348 (EA, K), fine tree 10–17 m. high, widespread in Somaliland chiefly in the Haud.

ITALIAN SOMALILAND. Bela on bank of Daua R., frt., June 1893, *Ruspoli & Riva* 1466 (1620) (638) (FI, lectotype). Cavennay, frt., Jan. 1893, *Ruspoli & Riva* 1078 (1189) (281) (FI, paratype). Abdallah, fl., 1891, *Keller* 222, 225 (Z, syntypes of *T. kelleri*).

KENYA. Northern Frontier Dist., Ajao Hill nr. Buna, alt. 800 m., frt., Jan. 1949, *Dale* 745 (EA, K).

Taxonomic history

Numerous specimens (including material of *T. prunioides* and *T. spinosa*) have been misidentified 'as *T. polycarpa* e desc.', '*T. kelleri* e desc.' or '*T. somalensis* e desc.'. It was not until the type specimens of these three species were compared that this confused state of affairs could be cleared up.

The type material of *T. kelleri* (*Keller* 222!, 225!) consists of flowering specimens, whilst that of *T. polycarpa* (*Ruspoli & Riva* 1466 (1620 (638))!, 1078 (1189 (281))!) has immature fruits; this made comparison difficult. However, by comparing the length of the spur-shoots, type of indumentum, general shape of the leaves, details of nerves and venation, and length of inflorescence, it was decided that they could not be maintained as separate species. Also, several specimens from British Somaliland provided a complete range from the early flowering stage to mature fruits which showed that *T. kelleri* could only be the flowering state of *T. polycarpa*, which is, in fact, a very variable species.

The name *T. polycarpa* was maintained rather than *T. kelleri*, although they were published at the same time, because fruits show much more clearly and more reliably than the flowers the differences between the species of *Terminalia*.

Distribution and ecology

T. polycarpa is distributed throughout eastern British Somaliland, and extends into central and southern Italian Somaliland, and into the Northern Frontier District of Kenya. It occurs in the areas occupied by *Acacia*, desert–grass savannah.

IMPERFECTLY KNOWN SPECIES BELONGING TO GROUP I ('SPINOSA' GROUP)

T. somalensis Engl. & Diels*—close to *T. brevipes*, but differing in the very irregularly branched, stout, tortuous long shoots, the longer spur-shoots (1–1·5 cm. long) and in the absence of spines; the fruits are also very different. According to the original description the inflorescence is sericeous-tomentose, thus differing from the glabrous inflorescence of *T. brevipes*.

Type material = *Hildebrandt* 1529 (fl., not seen), *Robecchi Bricchetti* 126 (FI, frt., lectotype). *Bally* 9077 from Kenya is conspecific with *Robecchi Bricchetti* 126.

T. robecchii Chiov.†—close to *T. spinosa*, differing only in the dense pubescence of the leaves and young branchlets, Abyssinia, Ogaden, *Robecchi Brichetti* 324 (FI, st., holotype).

Terminalia sp. 3—similar to *T. brevipes* in the slender branchlets, but differing in the smaller, narrowly obovate leaves (1·9 × 0·9–2·8 × 1·6 cm.), the conspicuous nerves and venation, shorter inflorescence (3–4·5 cm. long), tomentose flowers, and oblong-elliptic fruits (2·5 × 1·3 cm.). Abyssinia, Ogaden: *Ellis* 107, 165, *Simmons* 63 (all flowering specimens). *Lieut. Hummell* 139 (frt.).

Terminalia sp. 4—close to sp. 3, but differing in the stouter branchlets and longer spur shoots; the leaves are broadly obovate (2·8 × 1·5–3·9 × 2·2 cm.) glabrous, glaucous beneath, nerves and venation scarcely visible. British Somaliland: *Glover & Gilliland* 354 (frt.). Abyssinia: *Simmons* 5 (fl.).

(10) **T. erici-rosenii** R. E. Fries, *Wiss. Ergebn. Schwed. Rhod.-Kongo Exped.* 1911–12, **1**, 173, t. 9 (1914); Engl., *Pflanzenw. Afr.* **3** (**2**), 724 (1921).

See Fig. 10. Small tree, 5–12 m. high, with striated bark, bark of branchlets greyish black, velutinous-tomentose, peeling off to reveal reddish brown, striated, inner bark, which becomes greyish brown with age. Young shoots densely sericeous-tomentose. *Lvs.* broadly obovate, apex rounded to subtruncate and usually very shortly acuminate or mucronate, occasionally emarginate, base acute to cuneate, decurrent, 8·5 × 5·8–13 (–25) × 7 (–14) cm., densely and softly sericeous-tomentose on both surfaces, chartaceous; *upper surface*: midrib ± flattened, secondary nerves slightly raised, tertiary nerves ± impressed, venation scarcely visible; *lower surface*: midrib ± flattened, secondary and tertiary nerves conspicuous but not raised, venation obscurely reticulate; petiole 1–2 cm. long. *Infl.* 6–8 cm. long, peduncle 2 cm. long, densely velutinous-tomentose; *fl.*: lower receptacle densely velutinous-tomentose, upper receptacle sparsely pilose, but ± glabrous towards calyx-lobes; calyx-lobes acuminate. *Frt.* mostly elliptic-oblong, apex obtuse to rounded, emarginate, base subacute to subtruncate, 3·5 × 1·7–4 × 2·2 cm., finely tomentose; pedicel 0·5–0·7 cm. long.

The amount of material available is too small to judge the degree of variation in this species; however, the leaves do show rather large differences in size, but not in shape; the fruits seem to remain fairly constant.

NORTHERN RHODESIA. Abercorn Dist., nr. Lunzua R., W. of Mayne's Farm, alt. 1700 m., frt., May 1936, *Burtt* 6187 (BM, EA, K), in savannah country, tree 8 m. high with silvery leaves. Id., Lunzua Valley, alt. 1800 m., frt., May 1936, *Burtt* 6189 (BM, K), locally common on soils seasonally saturated and boggy, with *Combretum psidioides* and *Protea* spp., tree 7 m. high with striated bark and silvery foliage. Mporokoso Dist., Kalungwishi R., between Lake Bangweulu and Lake Tanganyika, fl., Oct. 1911, *Fries* 1155 (UPS, holotype). Chinsali Dist., Shiwa Ngandu, alt. 1800 m., frt., Feb. 1937, *Trapnell* 1697 (K), on shallow seasonally-moist soil over sandstone, small tree 5–7 m. high with distinctive silvery foliage.

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* *Monogr.* **4**, 24, t. 10c (1900).

† *Bull. Soc. Bot. Ital.* p. 38 (1917).

Distribution and ecology

T. erici-rosenii is known only from the specimens cited above so that its known distribution is confined to the northern districts of Northern Rhodesia. Little is known of its ecological preferences but two collectors have independently recorded it as occurring on seasonally saturated soils.

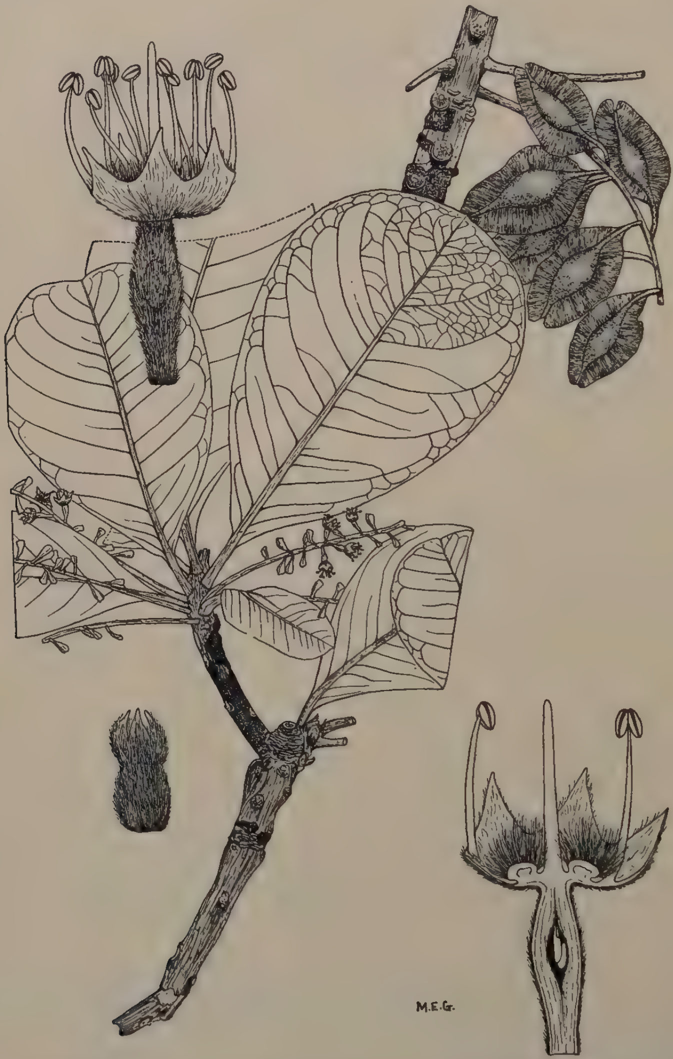

Fig. 10. *T. erici-rosenii* R. E. Fries. Flowering specimen from *Fries* 1155. Fruiting specimen from *Burtt* 6187.

(11) **T. brachystemma** Welw. ex Hiern, *Cat. Afr. Plants Welw.* **2**, 340 (1898); Engl. & Diels, *Monogr.* **4**, 20, t. 9 c (1900); Fries, *Wiss. Ergebn. Schwed. Rhod.-Kongo Exped.*, 1911–12, **1**, 174 (1914); Engl., *Pflanzenw. Afr.* **3** (**2**), 724 (1921); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, **2**, 147 (1954).

T. baumii Engl. & Gilg in Warb., *Kunene-Sambesi Exped.* p. 321 (1903); Engl., *Jahrb.* **39**, 514 (1907); Engl., *op. cit.* 724 (1921), synon. nov.

See Fig. 11. Small tree, 5–8 m. high; bark of bole grey, deeply and longitudinally fissured; bark of branchlets purplish brown or purplish black, glabrous, shining, peeling to reveal light brown, striated, inner bark. Young shoots glabrous. *Lvs.* broadly obovate to broadly oblanceolate, apex obtuse to rounded, occasionally very shortly cuspidate, base acute, sessile, 9 × 5–15 × 7 cm., glabrous, thinly coriaceous, glaucous beneath; *upper surface*: midrib ± flattened, secondary and tertiary nerves ± raised, venation scarcely visible; *lower surface*: midrib subprominent or flattened, secondary and tertiary nerves conspicuous but not raised, venation finely and obscurely reticulate. *Infl.* 7·5–11 cm. long, peduncle 3·5–4·5 cm. long, glabrous or sparsely to densely sericeous-tomentose; *fl.*: lower receptacle glabrous or sparsely to densely sericeous-tomentose, upper receptacle glabrous or sparsely pilose at base; calyx-lobes acuminate. *Frt.* ± elliptic to elliptic-oblong, apex obtuse to rounded, emarginate, base acute to rounded, 4 × 2·3–5·5 × 2·5 cm., glabrous, reddish brown; pedicel 0·5–0·7 cm. long.

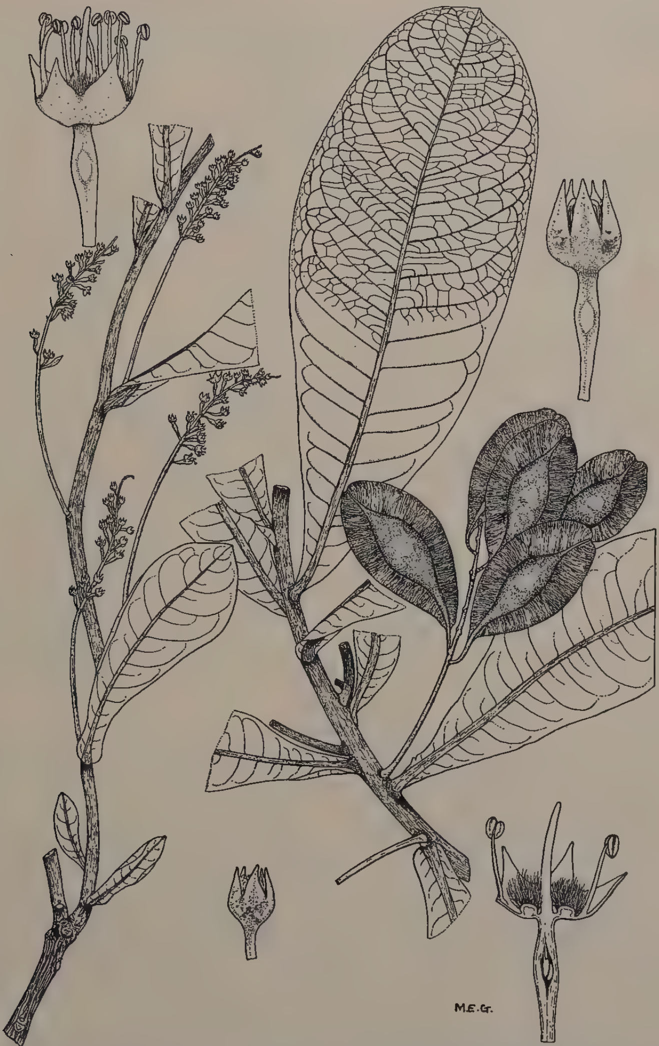

Fig. 11. *T. brachystemma* Welw. ex Hiern. Flowering specimen from *White* 3469. Fruiting specimen from *Miller* B 505.

T. brachystemma, in the strict sense, is not particularly variable, the leaves vary in length but the length to breadth ratio does not show any appreciable difference so that the general shape of the leaves remains more or less constant; the fruits show only slight variation in size and shape. The amount of indumentum of the inflorescence differs markedly—see under 'taxonomic history'.

BELGIAN CONGO. Haut Lomani Dist., Lunda, frt., Dec. 1933, *Lynes* 273 (BR). Haut Katanga Dist., Keyberg, 8 km. S. of Elisabethville, frt., May 1949, *Schmitz* 2409 (BR), tree in open forest. Lualaba Dist., Dilolo, frt., Jan. 1950, *Schmitz* 2685 (BR), tree nr. stream in degraded gallery forest.

TANGANYIKA TERRITORY. Tabora Dist., nr. Kilumbi on Chunya-Itigi Rd., alt. 1940 m., frt., May 1951, *Eggeling* 6089 (K), tree 7 m. high, leaves pale beneath, frt. reddish green.

SOUTHERN RHODESIA. Bubi Dist., Bakumbusi, about 80 km. N. of Bulawayo, on Dromoland Estate, frt., June 1947, *Keay* FHI 21305 (FHO), open savannah, on sandy soil on gentle slope below high level *Brachystegia* woodland, tree 5–8 m. high. Bulawayo Dist., hillside nr. Bulawayo, in granite kopje country, Mr Nevelle Jones's garden, frt., May 1947, *Keay & N. Jones* FHI 21274 (FHO), tree 8 m. high. Wankie Dist., Wankie, fl., Oct. 1929, *Pardy* 4685 (FHO).

NORTHERN RHODESIA. Livingstone Dist., Machili, frt., Feb. 1952, *Fewdays* 18 (FHO), small tree. Mwinilunga Dist., 1 km. S. of Matonchi Farm, fl., Oct. 1937, *Milne-Redhead* 2840 (K), in *Brachystegia* woodland at edge of lateritic grassland; tree 7 m. high, spreading branches, bark peeling off twigs, leaves light green, fls. yellowish white. Lealui Dist., Mongu, alt. 1130 m., frt., June 1933, *Trapnell* 1269 (K), in fringing *Burkea* bush and in fringing *Burkea–Erythrophleum* regeneration on Kalahari Sand, small tree 5–8 m. high. Kalabo Dist., on Kalahari Sand nr. Kalabo Boma, frt., Feb. 1952, *White* 2082 (FHO), in *Parinari curatellifolia–Brachystegia spiciformis–Pseudolachnostylis* woodland; tree 10 m. high, 0·3 m. dbh, crown light, lower branches spreading out almost at right angles; bark on bole and main branches thick, deeply fissured, grey, prominently ridged producing an open lattice effect; young branches and branchlets and branches of young trees rust coloured; leaves dull blue-green above, pale grey-green beneath, glabrous; frt. purple-red. Balovale Dist., on Kalahari Sand nr. Chitokaloki Mission, fl., Oct. 1952, *White* 3469 (FHO), with *Amblygonocarpus*, *Erythrophleum africanum* and *Bauhinia mendonçae*; small tree 6 m. high with white fls.

BECHUANALAND PROTECTORATE. Bamangwato Reserve, Lesuma Valley nr. Kazungula, frt., May 1947, *O. B. Miller* B505 (FHO, K), tree 8 m. high.

ANGOLA. Bié Dist., Chilanda, nr. Cassinga, alt. 1300 m., fl., Nov. 1899, *Baum* 215 (BM, K, isotype of *T. baumii*). Lunda Dist., Xa-Sengue, alt. 1200 m., frt., Apr. 1937, *Exell & Mendonça* 256 (BM), shrub 3 m. high, bark reddish. Malange Dist., Quizenga, on road to N'Bango, frt., 1903, *Gossweiler* 1311 (BM), tree to 8 m. high. Bié Dist., between Vila da Ponte (Fort Princess Amelia) and Cubango R., fl., Sept. 1905, *Gossweiler* 2030 (BM, K), small shrub 2 m. high, in dense thickets on ferruginous stony soil. Huila Dist., between Lopollo and Empalanca, alt. 1300–1800 m., frt., Oct. 1859, *Welwitsch* 4287 (BM, K, syntype), in open woods in stony places; same locality, fl., frt., May 1860, *Welwitsch* 4345 (BM, K, lectotype).

TRANSVAAL. Waterberg Dist., on Nooitgedacht farm, nr. Ypres Halt, frt., Nov. 1931, *Galpin* 11582 (K), in wooded grassland, tree 7 m. high. Id., Mosdene, nr. Naboomspruit, fl., Nov. 1931, *Galpin* 11583 (K), on sand dune, tree 5 m., high. Id., 14 km. N.E. of Nylstroom, alt. 1300 m., frt., May 1949, *Codd & de Winter* 5590 (K), in mixed bush on sandy flats, with *Terminalia sericea*, tree 5 m. high, leaves glabrous.

Taxonomic history

T. baumii was based on *Baum* 215!, which has glabrous flowers, whilst those of the type material of *T. brachystemma* are tomentose. Comparison of all flowering material from Angola and other territories showed that the amount of indumentum varies from almost glabrous, through sparsely pubescent, to densely tomentose. It, therefore, seems reasonable not to maintain *T. baumii* since this is the only difference which separates it from *T. brachystemma.*

T. silozensis Gibbs* (type = *Gibbs* 277 !, fl.) is doubtfully distinct from *T. brachystemma.*† The leaves are conspicuously smaller and narrower, and the general facies of *Gibbs* 277 suggests an intermediate between *T. brachystemma* and *T. sericea*, both of which occur together in the type locality of *T. silozensis*—the Matopos Hills in Southern Rhodesia. SRGH No. 29522, also from Matobo District, is very similar to *Gibbs* 277. *Lynes* 480, *Schmitz* 2603 and 1180 from the Haut Katanga District of the Belgian Congo closely resemble *Gibbs* 277, as do the following from Northern Rhodesia: *White* 2913 (Lusaka Dist.), *White* 2911, 2989 A (Feira District), and *White* 2933 (Mazabuka Dist.). This material is similar to *T. sericea* in leaf-shape but approaches *T. brachystemma* more closely in the glabrous and rather glaucous leaves, and the glabrous fruits.

More material and especially large samples and careful observations from populations of doubtful status are needed to test this hypothesis. It is also possible that these puzzling specimens may represent a small-leaved form of *T. brachystemma*, in which case the range of variation of the latter species would be extended.

Distribution and ecology

The centre of distribution of *T. brachystemma* is on the Kalahari Sands from Southern Rhodesia and Bechuanaland northward through eastern Angola and Barotseland to the southern parts of the Belgian Congo. In this region it is frequently dominant or co-dominant with *T. sericea* in narrow strips of stunted woodland fringing seasonally waterlogged depressions (*White*, field observations 1952, unpublished).

Elsewhere, off the Kalahari Sand, its precise distribution is uncertain. Many of the specimens from regions to the east of the Kalahari Sands are not typical and may represent hybrids with *T. sericea* (see above).

To the west of the Kalahari Sands in Benguela District of Angola (16) it is said to occur commonly with *T. sericea* on sandy soils in the area between Bailundo and Nova Lisboa, and on granite rocks near the coast at Catengue.

(12) **T. kaiserana** F. Hoffm., *Beitr. Kenntn. Flor. Centr. Ost-Afr.* p. 26 (1889); Engl. & Diels, *Monogr.* **4**, 19, t. 13 D (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 723 (1921); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr.), **2**, 145 (1949).

See Fig. 12. Shrub or small tree, 7–10 m. high, with fissured bark; bark of branchlets glabrous, shining, purplish brown to purplish black, peeling to reveal light brown, striated inner bark. Young shoots sparsely sericeous-tomentose or glabrous. *Lvs.* oblanceolate, ± lanceolate or narrowly elliptic, apex acute to shortly acuminate, occasionally mucronate, base acute to cuneate, 7·5 × 2·5–12 × 3 cm., young leaves sparsely sericeous-pubescent, soon becoming glabrous, chartaceous; *upper surface*: midrib flattened, secondary nerves ± impressed, tertiary nerves and venation scarcely visible; *lower surface*: midrib ± raised, secondary and tertiary nerves ± conspicuous but not raised, venation finely and obscurely reticulate; petiole (1 –) 1·5–3 (– 3·5) cm. long. *Infl.* 6·5–9·5 cm. long, peduncle 1·8–3 cm. long, usually glabrous, but occasionally very sparsely pubescent; *fl.*: lower receptacle usually glabrous but occasionally very sparsely pubescent, upper receptacle always glabrous; calyx-lobes subacuminate. *Frt.* ± broadly elliptic, apex obtuse to rounded, emarginate, base acute or obtuse to subtruncate, 4·8 × 2·5–5·5 × 2·8 cm., glabrous, purplish brown; pedicel 0·5–0·7 cm. long.

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* In *J. Linn. Soc.* (*Bot.*), **37**, 444 (1906).

† Since this account was written, much additional material has been received. *T. erici-rosenii*, *T. brachystemma*, *T. kaiserana*, *T. sericea* and *T. trichopoda*, although connected by intermediates, appear to be sufficiently distinct to be kept up, at least for the present, as species. *T. brachystemma* is remarkably uniform on the Central Kalahari Sands from the northern parts of the Bechuanaland Protectorate to the Kwango District of the Belgian Congo, and over most of this area it is the only member of the '*sericea*' complex to occur; here it has glabrous leaves, flowers and fruits, and if a narrow view of this species is taken it should be called '*T. baumii*'. Nearly all other specimens referred by Miss Griffiths to *T. brachystemma* (including the types) are variously intermediate between *T. baumii* and *T. sericea* (but closer to the former) and may represent hybrids and introgressants between them, but the matter can only be settled by careful field studies. The two specimens cited as *T. sessilifolia* belong to this intermediate complex. (F.W.)

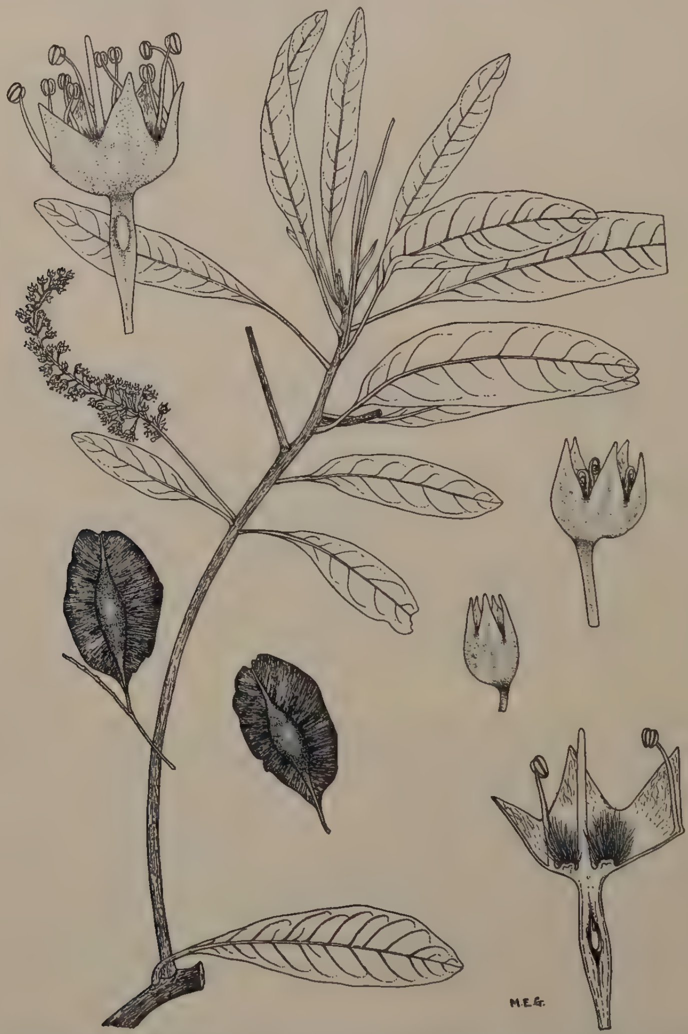

Fig. 12. *T. kaiserana* F. Hoffm. Flowering specimen from *White* 3676. Fruits from *Holmes* FH 2777.

The leaves vary markedly in length, although, on the whole, the general length to breadth ratio remains more or less the same; there is no appreciable variation in leaf-shape other than that mentioned in the above description. The petiole varies in length considerably. The mature leaves and inflorescence are consistently glabrous.

TANGANYIKA TERRITORY. Chunya Dist., N. Lupa R., alt. 1700 m., fl., Nov. 1947, *Groome* FH 2240 (EA, FHO), scattered second-storey tree. Mpanda Dist., Mpanda, frt., 1949, *J. Holmes* FH 2777 (FHO). Tabora Dist., Kaliuwa Village, alt. 1000 m., fl., Sept. 1950, *Shabani* 16 (FHO, K), tree with white fls. Mwanza Dist., Rumala, Hemera, alt. 1300 m., fl., Dec. 1953, *Tanner* 1876 (K), on deep sand on old cultivation site, growing in groups, coppiced tree 8 m. high with corrugated bark and aromatic white fls. Between Zanzibar and Uyui (tribal area in Tabora Dist.), fl., *Rev. E. Taylor* s.n. (K). Morogoro Dist., precise locality not given, frt., Feb. 1932, *Wallace* 361 (K), tree 27 m. high.

NYASALAND. North Nyasa Dist., Karonga, st., Mar. 1954, *Jackson* 1246 (FHO). Chisasa, fl., *Lewis* 75 (FHO), in *Brachystegia* forest on sandy soil at hill-foot.

NORTHERN RHODESIA. Abercorn Dist., 32 km. from Abercorn on Abercorn-Mpulungu Rd., alt. 1170 m., fl., Nov. 1950, *Bullock* 3493 (FHO, K, neotype), common in open '*miombo*' woodland, shrub or slender tree to 7 m. high, with pale green leaves and white fls. Id., on Mpulungu Rd., nr. Lunzua R., fl., May 1931, *O. B. Miller* D130 (FHO). Id., 2 km. E. of Mpulungu, fl., Nov. 1952, *White* 3676 (FHO), small tree 7 m. high, with white fls., in small population growing on old terrace-alluvium nr. Lake Tanganyika.

Taxonomic history

The type specimen (*Böhm* 141a from Tanganyika) has not been seen, but the species known under the name of *T. kaiserana*, some material of which has been collected near the type locality (Gonda or Igonda, south of Tabora), agrees with the type description and with the illustration in Engler and Diels's monograph.

T. kaiserana is very close to *T. sericea* but differs in the following characters: glabrous leaves and inflorescence; frequently longer inflorescences, with more laxly arranged flowers; longer petioles, 1–4 cm. long (in *T. sericea* very rarely exceeding 1 cm. in length).

Until recently it was possible to separate, on the glabrous character alone, all the available material into either one species or the other. However, two flowering specimens have recently become available which are intermediate between these two 'species' in the amount of indumentum on the leaves and inflorescence. The specimens are *Bullock* 1251 (Chiengi District, Northern Rhodesia) and *Shabani* 48 (Tabora District, Tanganyika).

Without a knowledge of the variability of the populations in the field, the precise status of such specimens must remain conjectural. It is possible that *T. kaiserana* has only recently been differentiated from *T. sericea* through geographical isolation (see Fig. 29). Their ranges overlap slightly to-day, so that, if there are no barriers to crossing, hybridity and introgression are likely to occur. If it is found that such intermediates are numerous it may be more satisfactory to treat *T. kaiserana* as a subspecies of *T. sericea*.

Distribution and ecology.

T. kaiserana has a very limited distribution, occurring most abundantly in the triangular area marked by the Lakes Victoria, Tanganyika and Nyasa; its southern limit is in the northern region of Nyasaland, and its eastern limit is in the Morogoro District of Tanganyika.

(13) **T. sessilifolia** R. E. Fries,* *Wiss. Ergebn. Schwed. Rhod.-Kongo Exped.* 1911–12, **1**, 174 (1914); Engl., *Pflanzenw. Afr.* **3** (2), 724 (1921).

See Fig. 13. Small tree, 9 m. high; bark of branchlets glabrous, shining, purplish black, peeling to reveal light brown, striated, inner bark. Young shoots pubescent, soon becoming glabrous. *Lvs.* obovate or ± lyrate, apex obtuse to rounded and shortly cuspidate or mucronate, base acute to cuneate, subamplexicaul, sessile, 8·5 × 3·5–12·5 × 4·5 cm., young leaves sericeous-tomentose, becoming glabrous or remaining sericeous-pubescent on midrib above, chartaceous; *upper surface*: midrib flattened or with central furrow, secondary nerves ± raised, tertiary nerves and venation scarcely visible; *lower surface*: midrib subprominent or flattened, secondary and tertiary nerves ± conspicuous but not

* See note at foot of p. 849.

raised, venation finely and obscurely reticulate. *Infl.* 9–11·5 cm. long, peduncle 3·5–4·5 cm. long, sericeous-tomentose; *fl.* lower receptacle densely sericeous-tomentose, upper receptacle tomentose at base, almost glabrous towards calyx-lobes; calyx-lobes acuminate. *Frt.* unknown.

NORTHERN RHODESIA. Abercorn Dist., Msisi nr. Abercorn, fl., Nov. 1911, Fries 1328 (UPS, holotype). Kawambwa Dist., nr. Kawambwa Boma, fl., Oct. 1952, *White* 3547 (FHO), small tree 9 m. high with white fls., with *Bridelia micrantha, Rubus* sp., *Anthocleista kerstingii* in small remnant of seepage *mushitu* (swamp forest).

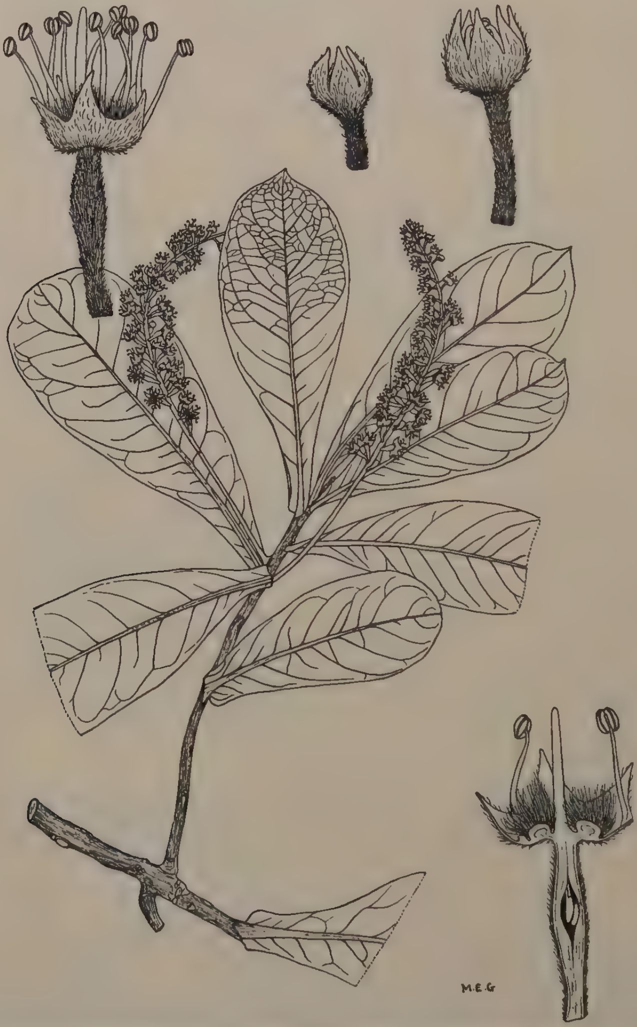

Fig. 13. *T. sessilifolia* R. E. Fries. Flowering specimen from *White* 3547.

Distribution and ecology

T. sessilifolia is known only from the two flowering specimens cited above, from which it would appear to be confined to the Abercorn and Kawambwa districts of Northern Rhodesia. It is closely related to *T. brachystemma*, but occurs outside the known distribution of that species, and the available information indicates that its habitat preferences are quite different.

(14) **T. sericea** Burch. ex DC., *Prod.* **3**, 13 (1828); Laws., *Fl. Trop. Afr.* **2**, 416 (1871); Sond. in Harv. & Sond., *Fl. Cap.* **2**, 507 (1894); Hiern, *Cat. Afr. Plants Welw.* **2**, 338 (1898) incl. var. *huillensis*, and var. *angolensis* pro parte, excl. *Welw.* 4285, 4343, 4339, and 4340; Engl. & Diels, *Monogr.* **4**, 20, t. 13C (1900); Engl. & Gilg in Warb., *Kunene-Sambesi Exped.* p. 321 (1903); Lugard & N. E. Brown, *Kew Bull.* p. 110 (1909); Baker f. *J. Linn. Soc.* (Bot.), **40**, 70 (1911); Engl., *Pflanzenw. Afr.* **3** (**2**), 724 (1921); Obermeyer, Schweickerdt & Verdoorn, *Bothalia*, **3**, 247 (1937); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr.), **2**, 145 (1949); Brenan, *Mem. N.Y. Bot. Gard.* **8**, 437 (1954); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, 2, 147 (1954); non *T. sericea* Cambess. (1829).

T. angolensis O. Hoffm., *Linnaea*, **43**, 131 (1881).
T. angolensis Welw. ex Ficalho, *Bol. Soc. Geogr. Lisb.* (2), 708 (1882), *Pl. Uteis*, p. 182 (1864).
T. fischeri Engl., *Pflanzenw. Ost-Afr.* **C**, 294 (1895).
T. nyassensis Engl., *op. cit.* 294 (1895).
T. brosigiana Engl. & Diels, *Not. Bot. Gart. Berl.-Dahl.* **2**, 191 (1898).
T. bubu De Wild. & Ledoux, *Contrib. Fl. Katanga*, Suppl. **2**, 84 (1929) excluding *Delevoy* 354, synon nov.

See Fig. 14. Shrub or small bushy tree, 3–12 m. high, occasionally to 16 m. high; bark of bole grey-brown or pale brown, deeply fissured longitudinally; slash pale-yellow; bark of branchlets purplish black, glabrous, shining, peeling to reveal light brown, striated, inner bark. Young shoots densely sericeous-tomentose. *Lvs.* oblanceolate to narrowly elliptic, apex acute to rounded, occasionally shortly acuminate, frequently mucronate, base acute to cuneate, 5·5 × 1·5–12·5 × 4·5 cm., young leaves densely sericeous-tomentose, becoming sparsely sericeous-pubescent to subglabrous (but midrib remaining tomentose), chartaceous; *upper surface*: midrib flattened, secondary nerves ± raised, tertiary nerves and venation scarcely visible; *lower surface*: midrib ± raised, secondary and tertiary nerves ± conspicuous but not raised, venation finely and obscurely reticulate; petiole 0·2–1 cm. long. *Infl.* 5–7·5 cm. long, peduncle 2·5–3 cm. long, densely sericeous-tomentose; *fl.*: lower receptacle densely sericeous-tomentose; upper receptacle less so; calyx-lobes acuminate. *Frt.* ± broadly elliptic, apex obtuse to rounded, usually emarginate, base obtuse to subtruncate, 3 × 1·75–5·5 × 3 cm., finely tomentose, purplish red to brown; pedicel 0·5–0·7 cm. long.

T. sericea shows considerable variation in the shape of the leaves, varying from narrowly obovate or elliptic-oblong to narrowly obovate-oblong, but nearly always narrowed from above the middle to the base which is usually cuneate. Leaf-size ranges from about 3 × 1·5 cm. to 14 × 5 cm. The amount of indumentum of the leaves varies with age, but even when the fruits attain maturity some of the silky hairs persist, particularly along the midrib on the upper surface. The fruits show no appreciable variation in size or shape.

Belgian Congo. Tanganyika Dist., Kabalo, fl., frt., July 1921, *Delevoy* 144 (BR, syntype of *T. bubu*). Haut Katanga Dist., without precise locality, fl., July 1949, *Delvaux* 1 (BR), tree 15 m. high, 6 m. to first branch, diam. 1·04 m. at 1·5 m., in closed savannah. Lualaba Dist., Kanda, fl., Sept. 1933, *Lynes* 58 bis (BR).

Tanganyika Territory. Singida Dist., Mkalama, fl., Nov. 1925, *Burtt* 340 (K), common bush or tree in *Acacia tortilis* and *Brachystegia* woodland, especially by sandy river-courses. Ulanga Dist., Kiberege, alt. 400 m., fl., Dec. 1934, *Culwick* 1 (K), tall straggly tree in thick bush and forest along sides of Ulanga Valley, not found higher than about 700 m. alt. Dodoma Dist., Meia Meia, alt. 1170 m., frt., Aug. 1928, *Greenway* 794 (K), fairly common, on grey sandy loam; tree 10 m. high. Tabora Dist., Malongwe Issuri Sawmills, frt., Feb. 1952, *Hughes* 156 (FHO, K), tree 12 m. high, 0·3 m. diam., with bright red frt. Ufipa Dist., Rukwa Rift, fl., Nov. 1933, *Michelmore* 714 (K), tree with moderately scented white fls.

PORTUGUESE EAST AFRICA. Quissango Dist., mouth of Msalu R., fl., Oct. 1911, *Allen* 81 (FHO, K), on sandy hill, tree 13 m. high. Chimoio Dist., along Revue R., frt., Mar. 1948, *Mendonça* 573 (BM), in open secondary woodland; small tree 4–5 m. high. Maputo Dist., between Umbeluzi and Porto Henrique, fl., Nov. 1944, *Mendonça* 2841 (BM, K), in savannah, tree 10 m. high. Between Muatize and 226 km. along railway, frt., May 1948, *Mendonça* 4114 (BM, K), tree 8–10 m. high. Marracuene Dist., Lourenço Marques, alt. 50 m., Dec. 1897, *Schlechter* 11596 (BM, K).

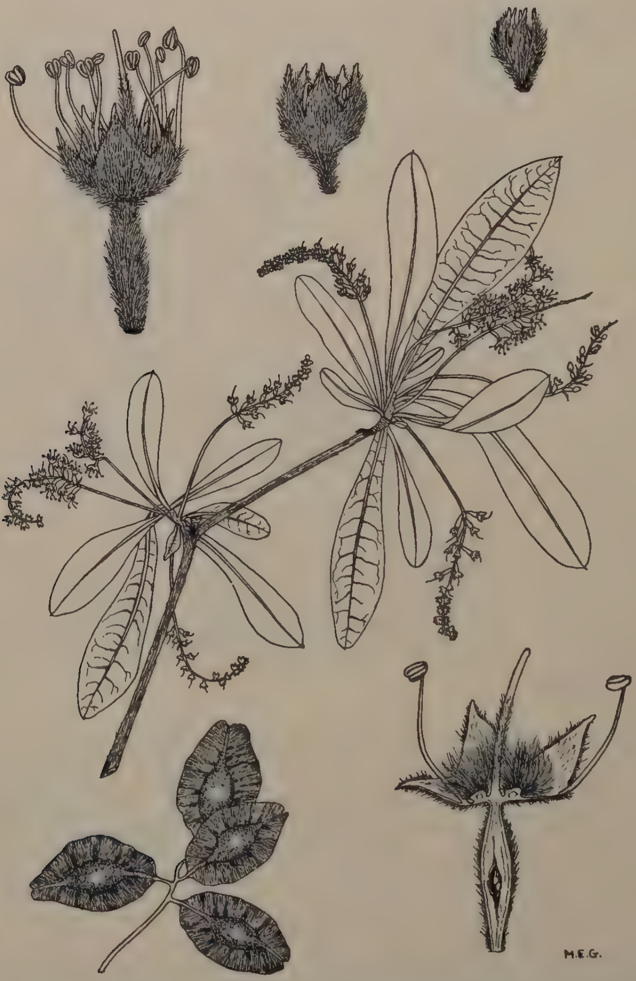

Fig. 14. *T. sericea* Burch. ex DC. Flowering specimen from *Morze* 5c. Fruiting specimen from *Mullin* 31/51.

NYASALAND. Kota-Kota Dist., Kasabula's Village, alt. 1000 m., frt., Aug. 1946, *Bras* 17123 (BM, K), scattered on open ridges, tree 15 m. high, 0·3 m. diam., bark rough foliage grey. Kasungu Dist., Kasungu, alt. 1000 m., st., Aug. 1946, *Brass* 17410 (K common tree in *Brachystegia* woodland, 10–12 m. high, 0·3–0·35 m. diam., grows to muc larger size on moist sandy soil, foliage greyish. Blantyre Dist., Shire Highlands, fl., 189

Buchanan 189 (BM, K, isotype of *T. nyassensis*). Zomba Dist., precise locality not given, fl., *Clements* 678 (FHO). Mlanje Dist., Tuchila Plain, fl., *Topham* 938 (FHO).

SOUTHERN RHODESIA. Umtali Dist., Commonage Sand Quarry, alt. 1200 m., fl., Nov. 1954, *Chase* 5342 (FHO), tree 6 m. high with straight bole, bark rough, grey, leaves silvery, fls. small, scented, white. Salisbury Dist., Salisbury, alt. 1700 m., fl., Nov. 1919, *Eyles* 1883 (K), bushy tree 5–7 m. high, fls. pale green to white. Bulalima-Mangwe Dist., Plumtree, fl., Jan. 1955, *Meara* 14 (FHO). Chilimanzi Dist., 6 km. form Umvuma on Gwelo Rd., frt., Feb. 1951, *Mullin* 31/51 (FHO), nr. termite mound, tree 4 m. high. Mtoko Dist., nr. Mudzi R., 80 km. E. of Mtoko, fl., Nov. 1950, *Whellan* 476 (FHO).

NORTHERN RHODESIA. Sesheke Dist., Masese, frt., Dec. 1952, *Angus* 1020 (FHO), with *Baphia obovata*, *Bauhinia*, *Acacia*, etc., at edge of *Baikiaea* '*mutemwa*'; tree 10 m. high; 0·25 m. dbh, bark fibrous, deep longitudinal furrows, pale brown, frt. reddish brown. Mazabuka Dist., foot of Kabanda Hill, frt., Apr. 1953, *Bainbridge* 10/53 (FHO), on red granite soil in *Kirkia acuminata*, *Lannea* spp., *Sterculia quinqueloba* thicket with thick undergrowth; tree 8 m. high, bark brown, with typical twist of longitudinal fissures, bark on twigs smooth, frt. plum-coloured. Livingstone Dist., at edge of Katombora forest nr. Zambezi swamp, lower road from Katombora to Kazungula, fl., frt., Oct. 1947, *Morze* 5c (FHO). Petauke Dist., streamside on Great East Rd., 16 km. E. of Luangwa R., fl., Nov. 1932, *Stevenson* 472 (FHO). Livingstone Dist., Dambwa F. R., 8 km. N. of Livingstone, frt., Jan. 1952, *White* 1884 (FHO), growing at dambo-edge on Kalahari Sand, small tree 3 m. high.

BECHUANALAND PROTECTORATE. Batawana Reserve, Maun camp on bank of Thamalakan R., st., June 1937, *Erens* 327 (K), tree 5–7 m. high. Bangwaketsi Reserve, Kanye, Mokyodumo Valley, about 10 km. E. of Pharing, alt. 1300 m., fl., Nov. 1948, *Hillary & Robertson* 533 (K), small tree 3–7 m. high. Bamangwato Reserve, T'klakane Pitts N.W. of Chukutsa Pan, alt. 840 m., frt., Oct. 1899, *Lugard* 306 (K), common scrub bush of the Kalahari Desert occurring in waterless regions, usually a bush up to 2 m. high, but sometimes grows to a tree 7 m. high, fls. greenish white. Kazungula, fl., Nov. 1935, *O. B. Miller* B86 (BM, FHO). Bakhatla Reserve, Mochudi, frts., Mar. 1914, *Rogers* 6616 (BM).

ANGOLA. Bié Dist., between Micango and Kuiriri R., frt., Feb. 1906, *Gossweiler* 3568 (BM), in open thickets, tree 3·5 m. high, leaves silvery-white on both surfaces, frt. purplish. Malange Dist., nr. Quela, fl., Sept. 1935, *Nolde* 91 (BM). Cuanze Norte Dist., nr. Caghuy, fl., Nov. 1856, frt., May 1857, *Welwitsch* 4286 (K, syntype of var. *angolensis*), in dry, thin, open woods. Huila Dist., between Lopollo and Nene, alt. 1700 m., fl. Dec. 1859, young frt. Feb. 1860, *Welwitsch* 4294, 4338 (K, syntypes of var. *huillensis*), in hilly, bushy, somewhat stony, dry and barren situations, small tree, foliage grey, fls. white.

SOUTH WEST AFRICA. Grootfontein Dist., Grootfontein, frt., Apr. 1913, *Engler* 6296 (K). Precise locality not given, frt., 1900, *Rautanen* 305 (K). Ovamboland Reserve, nr. Oshikango on Angola border, fl., Nov. 1947, *Rodin* 2619, 2707 (K), on flat, sandy soil in forest area, with *Colophospermum*, *Sclerocarya*, *Combretum*, *Spirostachys*, etc.; tree 10 m. high with white fls. Precise locality illegible, fl., Jan. 1886, *Schinz* 555 (K).

TRANSVAAL. Potgeitersrust Dist., about 11 km. N.E. of Gilliad, frt., June 1937, *Erens* 198 (K), in bushveld. Marico Dist., precise locality not given, fl., Dec. 1950, *Louw* 1888 (K), tree up to 5 m. high, usually with single bole, dominant on parts of sandy flats. Zoutpansberg Dist., Zoutpan, in *Lonchocarpus* belt, fl., Nov. 1932, *Obermeyer, Schweickerdt & Verdoorn* 1 (K), growing with *Rhus*, *Dichrostachys* and *Grewia*. Barberton Dist., Malelane, frt., Nov. 1919, *Phillips* s.n. (FHO), very occasional tree up to 10 m. high.

SWAZILAND. Hlatikulu Dist., nr. Usutu R., on Bremersdorp-Hlatikulu Rd., st., June 1938, *O. B. Miller* S/67 (BM, FHO). District unknown, on road to Stevsons, frt., May 1932, *Pole Evans* 3406 (64) (K). Bank of Mzimporu R., fl., Dec. 1931, *Pole Evans* 3417 (26) (K).

NATAL. Hlabisa Dist., nr. False Bay, fl., Dec. 1944, *Gerstner* 5227 (K), medium-sized tree.

British Bechuanaland. Vryburg Dist., plains N. of Mashowing R., between Olive Tree Station and Last Water Station, fl., Oct. 1812, *Burchell* 2330/3 (K). Id., between Chue Valley and Mashowing R., fl., Oct., 1812, *Burchell* 2399 (K, isotype). Id., Palmyra Farm, 96 km. N.E. of Vryburg, frt., Feb. 1948, *Rodin* 3542 (K), tree 13 m. high, in sandy open tree veld with *Combretum*, *Terminalia* and *Acacia*.

Taxonomic history

No specimens are cited for *T. angolensis* O. Hoffm. (from Malange, Angola, fl.), or for *T. brosigiana* (from Uluguru Mts., Tanganyika, fl.), both of which are placed as synonyms of *T. sericea* by Engler and Diels. Judging by the original descriptions this view is justified.

The type material of *T. fischeri* (*Fischer* 258, 259 from Salanda, Tanganyika, fl.) has not been seen, but it is cited by Engler and Diels as a synonym of *T. sericea*, and also the original description agrees with the latter species.

T. nyassensis was based on *Buchanan* 189! (Shire Highlands, Nyasaland, fl.), which comes well within the range of variation of *T. sericea*. It is cited as a synonym of *T. sericea* by Engler and Diels.

Hiern included *T. angolensis* Welw. ex Ficalho under his var. *angolensis*, based on *Welwitsch* 4339, 4286, 4340, 4341, 4342, 4285 and 4343 (the type material on which *T. angolensis* Welw. was based is not known, but presumably it includes some of the above numbers). *Welwitsch* 4343 and 4285 are excluded because they differ from *T. sericea* in the glabrous leaves and fruits, and appear to be intermediate between the latter species and *T. brachystemma*. *Welwitsch* 4339 and 4340 are also excluded; they are atypical in possessing very long spreading hairs on the branchlets, inflorescence axes and petioles. Both var. *angolensis* sens. strict. and var. *huillensis* are now included in *T. sericea* as they come within the range of variation of this species as currently circumscribed.

T. bubu was based on *Delevoy* 144! (fl., frt.) and *Delevoy* 354! (st.), both from Katanga in the Belgian Congo, and differs from *T. sericea* only in the apiculate apex of the fruits; according to the measurements of the authors the apiculate apex is 1 mm. long! An examination of the fruits of *Delevoy* 144 showed that most of the fruits have a slightly emarginate apex, and, in those with an apiculate apex, the latter represents the persistent style; this is not an uncommon feature of the fruits of *T. sericea*. *Delevoy* 354 is a young sterile shoot (? coppice shoot) and is atypical in leaf-shape and the indumentum of long spreading hairs.

Distribution and ecology

T. sericea is a very widespread species, occurring more or less throughout South Tropical Africa as far south as northern Natal; its northern limit is in the Lake Province of Tanganyika.

In Tanganyika it is rare in the *miombo* woodland regions occurring in the Mwanza area (5), and when it does occur it is very stunted, but it is a common species in the *miombo* regions of the Central Province. *Combretum–Ostryoderris–T. sericea* woodland is described from the Shinyanga region, and occurs on higher ground, or between *Brachystegia spiciformis* woodland and hard-pan alluvial sites. This type also occurs in the Central Province, fringing Itigi thicket, and along the margin of the Wembere Steppe, and at the foot of Bereku Ridge. In Shinyanga District (27) it forms part of the *Combretum zeyheri–T. sericea–Commiphora fischeri–C. pilosa* community, which occurs on broad ridges and slopes, and on well-drained plateau sites, and is said to replace *miombo* in these situations. In the Western Province around Kakoma (15) it is a common species at the edge of *mbugas*, and is one of the typical species in a 'semi-*mbuga*' type of mixed *miombo* with *Combretum* and *Terminalia*, with or without occasional termite mounds and *Afrormosia angolensis*.

In the Belgian Congo *T. sericea* occurs in the *miombo* woodland in Katanga, and is recorded by Duvigneaud (11) from Haut Kwango in the region between the Wamba and Loange Valleys, where it is found on sandy soils in open *Brachystegia–Isoberlinia* woodland (*tumbi* or *miombo*) which appears in this area to be more or less degraded from *Erythrophleum–Combretum* savannah woodland.

It occurs in the *miombo* woodland areas in Nyasaland and Portuguese East Africa, and also, in the latter territory, in the coastal savannah containing patches of evergreen forest and scrub.

In South Africa (1) *T. sericea* is a common species in the low veld, bush veld and bush savannah types of vegetations. In the low veld of the east, the deciduous tree savannah type on low ground at less than 670 m. alt. forms an open woodland on deeper soils with *T. sericea* and *Commiphora* spp. abundant; the former species is particularly abundant under drier conditions where the cover is more open. On kopjes, *mopane* may be absent and is replaced by *T. sericea–Combretum–Peltophorum* savannah woodland. The dry deciduous forest type at more than 800 m. alt., which occurs on foothills, may be replaced on the more exposed slopes by a savannah type in which *T. sericea* and *Pterocarpus angolensis* are abundant. The more open bush veld varies from a very open woodland to a closed bush formation on deeper soils. *Burkea africana* and *T. sericea* are the dominant species occurring on sandy soils. On sandy soils *B. africana* replaces *Acacia* spp. as the pioneer colonizer on areas cleared of grassland, but tends to decrease in quantity when the more dominant *T. sericea* becomes established. It also occurs in the drier bush savannah region of the west, in the Vryburg area, with an annual rainfall about 250–450 mm. (10–18 in.).

T. sericea occurs throughout the Kruger National Park (7) and shows a preference for the poorer sandy soils; it is particularly common near Pretorius Kop Gate, where it forms part of the large-leaved *Combretum–Terminalia* woodland, one of the five main types of vegetation occurring in the Park.

In Southern Rhodesia (17) *T. sericea*, associated with *Burkea africana*, is the dominant tree on sandstone and adjoining granite soils. It becomes more closely spaced and larger when found occurring near areas with a more permanent water supply, such as, near streams and seepage zones. It is the main constituent of the 'Mangwe' type of savannah, which occurs in the south-western part of the territory with an annual rainfall of 500–625 mm. (20–25 in.). It also occurs in *mukusi* woodland with *Pterocarpus angolensis* and *Burkea africana* and in the fine-leaved savannah north-west of Bulawayo.

In Northern Rhodesia (White, unpublished), it is widely spread in the drier southern half of the Territory, and occurs characteristically in pure or almost pure stands in narrow zones on sandy soils at the edges of seasonally waterlogged depressions ('dambos').

In Bechuanaland, O. B. Miller (25) suggests that areas where *Baikiaea plurijuga* and *T. sericea* occur together are probably the result of fire damage to the original *Baikiaea* forest. *T. sericea* with its more prolific and annual seeding, and its better method of seed dispersal seems to take advantage of the cleared ground, but owing to its more light-demanding habit will eventually disappear unless the succession is again disturbed. *Burkea africana* accompanies *T. sericea* as a pioneer colonizer in badly burnt woodland. In the southern Kalahari region (26) *T. sericea* is always dwarfed or forms a bushy coppice in the areas west of Kanye, where the woody flora rapidly becomes poorer in species as one travels westwards; *Acacia* spp., *Boscia albitrunca* and *Ziziphus mucronata* are the main components. Pole Evans (31) records *T. sericea* as being very common throughout Bechuanaland on sandy soils, occurring in the valley of the Notwani River in southern Bechuanaland with *Burkea africana*, *Combretum zeyheri* and *Sclerocarya caffra*; northwards, on deeper sands, the bush is frequently replaced by tree growth composed of large trees of *T. sericea*, *Burkia africana*, *Combretum imberbe* and *Strychnos pungens*. With *Burkia africana* and *Acacia* spp., *T. sericea* replaces *mopane* on the white sandy soils in the Mababe Flats area. On the sands abutting the north-west bank of Taoge River near the Okovango Pan considerable development of *T. sericea* has taken place.

Dinter (9) records *T. sericea*, in South West Africa, as one of the characteristic species of the 'Omaheke' formation which is found principally in such mountainous regions as Tsumeb, Bokoberge, Dijitjikaberge and Hüttenberg.

In Angola (16) it occurs throughout most of the *miombo* woodland areas and forms a *T. sericea* society on sandy clay soils.

IMPERFECTLY KNOWN SPECIES BELONGING TO GROUP II (A) ('SERICEA' GROUP)

The following species, 5–7, all possess on the second-year branchlets the blackish peeling bark which characterizes this group. They differ from all other species in the group but are represented only by single specimens. They are all from Northern Rhodesia.

Terminalia sp. 5. *Lvs.* elliptic-obovate, apex obtuse, base acute to subcuneate, densely covered with very short curly hairs beneath, less so above; 10 × 4·2–13·2 × 5 cm., subsessile. *Infl.* 10–10·5 cm. long. Young branchlets and infl. densely hairy. *Indumentum* differing markedly from the sericeous-tomentum of other species in the 'sericea' group. Mwinilunga Dist., *W. D. Holmes* 885 (FHO, fl.).

Terminalia sp. 6. *Branchlets* similar to *T. erici-rosenii*. *Lvs.* broadly obovate, apex ± truncate, and shortly and abruptly acuminate, base sharply cuneate; 9·5 × 6·5–20·5 × 14·2 cm., petiole 0·7 cm. long. *Infl.* about 9 cm. long. *Branchlets, lvs and infl.* densely hairy with indumentum of same type as in sp. 5. Mwinilunga Dist., *Angus* 539a (FHO, old fls.).

Terminalia sp. 7. *Lvs* similar in shape and size to *T. erici-rosenii* but almost glabrous, rather glaucous beneath. *Frts.* small, finely tomentose, 3 × 1·5 cm. Luwingu Dist., *Stevenson* 254 (FHO, frt.).

T. trichopoda Diels, in Engl., *Jahrb.* **39**, 514 (1907).

Closely related to *T. sericea* but with very much longer leaves and fruits. *Lvs.* obovate, elongate-obovate or broadly obovate-elliptic, apex shortly and broadly acuminate, base ± obtuse, 10·5 × 3·5–17·5 × 7 cm., petiole 1·5–2 cm. long. *Secondary nerves* prominent beneath. *Indumentum* on lvs. either coarsely tomentose or appressed sericeous-tomentose. *Infl.* 10·5–14 cm. long, fls. laxly arranged; *fl.*: lower receptacle densely tomentose, *not* silkly, upper receptacle sparsely tomentose; calyx-lobes *long*-acuminate. *Frt.* broadly oblong-elliptic to narrowly elliptic, 7 × 2·5–7·5 × 4·2 cm., finely tomentose; pedicel 1·5–2 cm. long. NYASALAND, Fort Johnston, *Jackson* 1691 (FHO, frt.). N. RHODESIA, Livingstone Dist., *Bourne* 21 (FHO, frt.). S. RHODESIA, Matobo Dist., *O. B. Miller* 1423 (fl.), *Plowes* 1441 (frt.); Nyamandlovu Dist., SRGH Nos. 42136 (fl.), and 42161 (frt.), collected from same tree.

T. trichopoda was based on *Engler* 2847a (Matopos) and *Engler* 3142 (Umtali), both fruiting specimens. The type specimens have not been seen, but, recently, numerous specimens have been collected in Southern Rhodesia from the neighbourhood of the Matopos, and these agree with the original description.

T. sericea and *T. trichopoda* occur together in the same locality, and several specimens which appear intermediate between these two species are thought to be hybrids; *Plowes* 1411 (young frt.) and *Plowes* 1349 (fl.) are two such specimens. This view is supported by field observations (Dr Wild). The leaves are smaller and narrower and the secondary nerves less prominent than in *T. trichopoda*; they gradually narrow to a cuneate base as in *T. sericea*.

(15) **T. scutifera** Planch. ex Laws., *Fl. Trop. Afr.* **2**, 417 (1871); Engl. & Diels, *Monogr.* 4, 25, t. 14 A (1900); Pobéguin, *Fl. Guinée Franç.* p. 178 (1906); A. Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); Engl., *Pflanzenw. Afr.* **3** (**2**), 726 (1921); Keay, *Fl. West Trop. Afr.* ed. 2, **1** (**1**), 277 (1954).

See Fig. 15. Tree, 7–15 m. high; bark of branchlets finely and longitudinally furrowed, light brown. *Lvs.* broadly oblanceolate to narrowly obovate, apex usually shortly acuminate, base acute, 8·5 × 3·2–18·5 × 7·8 cm., young leaves and buds densely ferrugineous-tomentose, older leaves glabrous or very nearly so, slightly revolute, thinly coriaceous, shining above, dull beneath; *upper surface*: midrib impressed, secondary and tertiary nerves and venation raised; *lower surface*: midrib and secondary nerves prominent, tertiary nerves and venation subprominent; petiole 1–1·8 cm. long. *Infl.* 4·5–8 cm. long. peduncle 2·5–3 cm. long, sparsely ferrugineous-tomentose; *fl.*: lower receptacle densely ferrugineous-tomentose, upper receptacle sparsely pubescent; calyx-lobes acute, reflexed in open flower; style pilose. *Frt.* subrhomboid; 2·5 cm. long, 3 cm. broad, wings narrow, about 0·4 cm. broad; sessile, sparsely pilose becoming glabrous, dark brown.

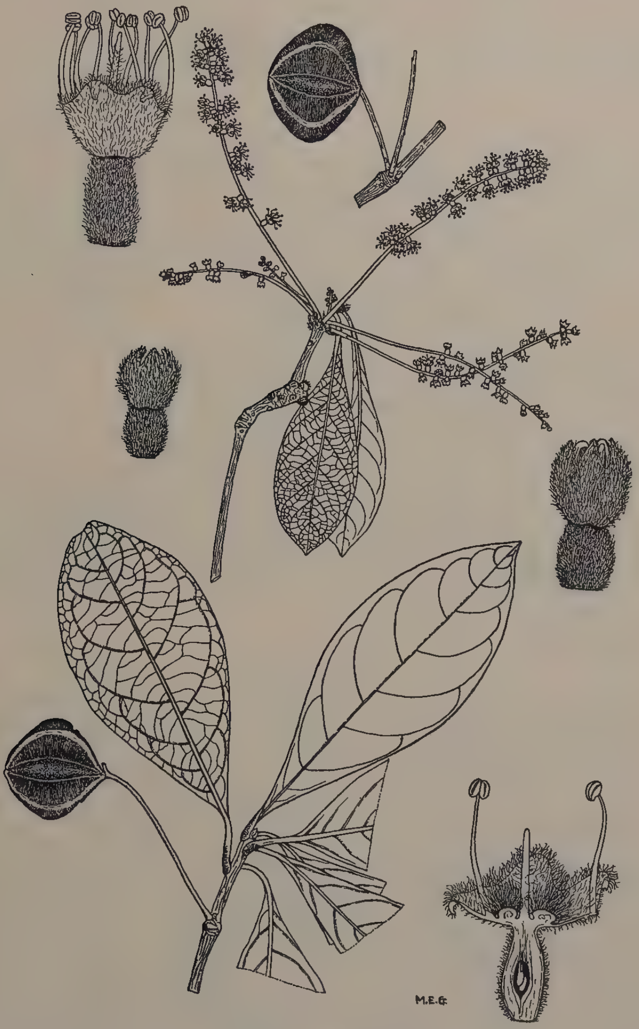

Fig. 15. *T. scutifera* Planch. ex Laws. Flowering specimen from *Lane-Poole* 87. Fruiting specimen from *Pelly* SLFD 151.

PORTUGUESE GUINEA. Bissau, Pefiné, fl., Jan. 1945, *Espírito Santo* 1703 (K), on gravelly ground in mangrove zone, deciduous tree 10 m. high with white fls. Formosa to

Porto de Alcóco, frt., Apr. 1945, *Espírito Santo* 1989 (K), in gravelly ground in mangrove zone, tree 12–15 m. high, very abundant in this region.

FRENCH GUINEA. Conakry, nr. the town, fl., June 1900, *Debeaux* 141 (K). No locality or date given, frt., *Heudelot* 907 (K, OXF, isotype).

SIERRA LEONE. Colony Prov., on sea shore at Kent, about 32 km. S. of Freetown, frt., Dec. 1922, *Dawe* 419 (K). Id., Lumley Beach between Aberdeen and Goderich, fl., Feb. 1927, *Deighton* 534 (BM, K), tree 7–8 m. high, branching from base, fls. when young leaves are appearing. Id., Hamilton, fl., Dec. 1911, *Lane-Poole* 87 (K), knotted and gnarled by sea shore, grows tall and straight in interior. Id., Cockle Bay (? Cockerill Bay just N. of Lumley), frt., Aug. 1937, *Pelly* SLFD 151 (FHO), tree 8 m. high on sand beach.

Distribution and ecology.

T. scutifera is a strictly West African species distributed from Portuguese Guinea to Sierra Leone. The available evidence suggests that it is confined to coastal habitats in areas occupied by mangrove swamp vegetation or freshwater swamp forest.

It is interesting to note that it is extremely closely related to *T. nyssaefolia* Britton, which occurs in the West Indies and northern South America, and occupies a similar habitat.

(16) **T. superba** Engl. & Diels, *Monogr.* **4**, 26, t. 14 B (1900); De Wild. & Dur., *Ann. Mus. Congo Belg. Bot., Sér.* **3**, Reliqu. Dewevr., fasc. **2**, 84 (1901); Th. & H. Dur., *Syll. Fl. Cong.* p. 195 (1909); Holland, *Kew Bull.* (Addit. Ser.), **9** (2), 307 (1911); A. Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); De Wild., *Miss. For. Agric. Compte J. de Briey au Mayumbe*, p. 204 (1920); Engl., *Pflanzenw. Afr.* **3** (2), 726 (1921); Pellegrin, *Fl. Mayombe* **1**, 116 (1924); De Wild., *Pl. Bequaert.* **4**, 343 (1928); Aubrév., *Fl. For. Côte d'Ivoire* **3**, 58 (1936); Kennedy, *For. Fl. Southern Nigeria*, p. 44 (1936); Burtt Davy & Hoyle, *Check-Lists For. Trees & Shrubs Brit. Emp.* **3** (Gold Coast), 36 (1937); Keay, *Fl. West Trop. Afr.*, ed. 2, **1** (**1**), 277 (1954).

T. altissima A. Chev., *Vég. Ut. Afr. Trop. Franç.* **5**, 151 (1909); A. Chev., *op. cit.* 256 (1920).

See Fig. 16. Tall straight-boled tree, up to 50 m. high, with strong, sharp, fairly wide and thin buttresses extending up the bole to about 3 m. and spreading straight out from it. Bole up to 20 m. high before first branch. In young and middle-aged trees branches arranged in ± conspicuous whorls spreading horizontally. In older trees the crown is flattish with a few horizontal branches confined to top of the bole. Bark of bole greyish fawn to blackish grey, ± smooth, or fissured longitudinally, flaking to reveal whitish surface which often turns reddish; bark of branches grey-brown with fine longitudinal fissures; slash pale yellow, OB reddish yellow, IB whitish, becoming brown. *Lvs.* broadly oblanceolate to narrowly obovate, or broadly oblong-elliptic, apex shortly acuminate or obtuse, base obtuse to acute, $10 \times 5{\cdot}5$–$12\ (-20) \times 6{\cdot}5\ (-8{\cdot}5)$ cm., glabrous, slightly undulate, thinly coriaceous, midrib and secondary nerves flattened above, prominent beneath, tertiary nerves not raised above or beneath, venation finely and obscurely reticulate, most conspicuous on lower surface; petiole 3–5 (−7) cm. long. *Infl.* 10–15 (−23) cm. long, peduncle 2·5–3 cm. long, glabrous or sparsely pubescent; *fl.*: lower receptacle densely sericeous-tomentose, upper receptacle sparsely sericeous-pubescent; calyx-lobes obtuse, reflexed in open flower; style pilose. *Frt.* transversely oblong-elliptic: 1·5–2·5 cm. long, 4–5·5 cm. broad; sessile, glabrous, straw-coloured when mature.

FRENCH GUINEA. Kissidougou, fl., Feb. 1909, *Chevalier* 20702 (K).

SIERRA LEONE. Dist. unknown, Bandama, fl., Feb. 1918, *Aylmer* 5791 (K), very large tree. Kenema Dist., Kambui Hills F. R., st., Nov. 1937, *Edwardson* 239 (FHO). Id., Hangha, about 9 km. N.E. of Kenema, fl., frt., Feb. 1914, *Lane-Poole* 146 (K), very large tree, bark rough, marked with black spots where branches come away. Tonkolili Dist., Tonkoli F. R. nr. Sumbaria, 4 Jan. 1954, 29 Jan. 1954, 12 Mar. 1954, all fruiting specimens from tree 'TK I' coll. by *Ranger Yongawo* (FHO), on level site in high forest. Id., same dates, all fruiting specimens from tree 'TK II' coll. by *Ranger Yongawo* (FHO), in high forest in valley.

Ivory Coast. Cercle de Abidjan, nr. station at Azaguié about 40 km. N.W. of Bingerville, st., Oct. 1909, *Chevalier* 22307 (K).

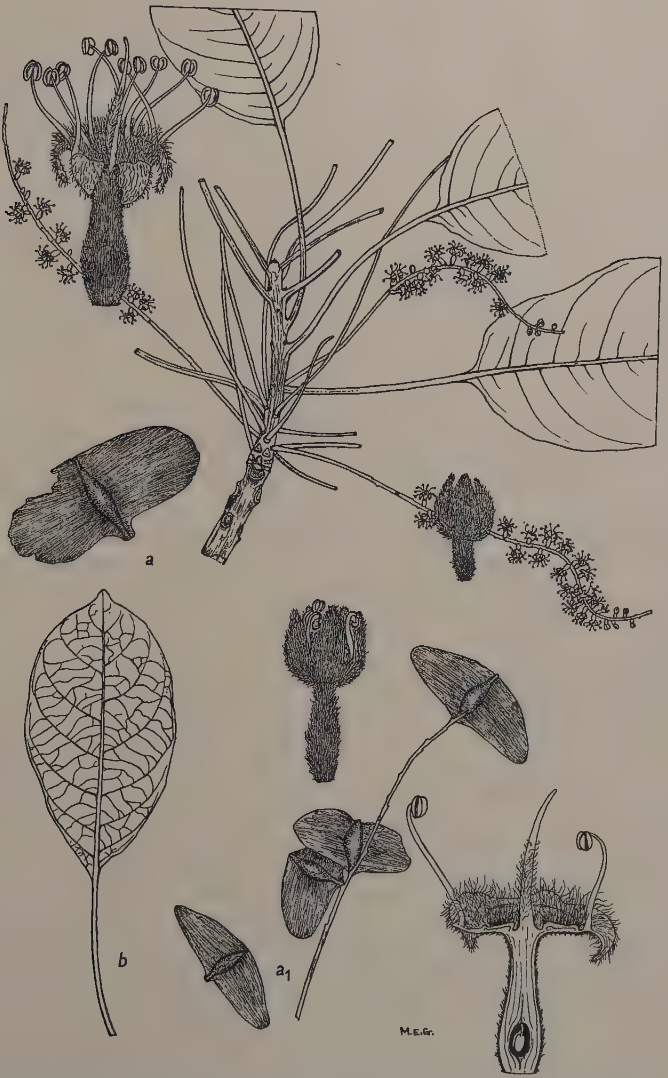

Fig. 16. *T. superba* Engl. & Diels. Flowering specimen from *Taylor L* 12. *a*, from *Vigne* 118; a_1, *b*, from *Jones & Onochie* FHI 16678.

Ghana. Wasaw-Aowin Dist., nr. Asankrangwa, fl., Jan. 1912, *Brent* 3 (K), tall tree with small yellow fls. Mampong Dist., Kumawu, alt. 470 m., frt., June 1913, *Chipp* 457 (K). Birim Dist., Kwahu, alt. 800 m., frt., Apr. 1900, *Johnson* 668 (K), large tree. Dist. unknown, Dunkwa, alt. 150 m., fl., frt., Feb. 1926, *Vigne* 118 (FHO), large tree, straight trunk, big buttresses, bark smooth, flaky; same locality, frt., June 1923, *Vigne* 878 (K).

NIGERIA. Omo and Shasha F. R., between Onysanya and Owesemele, frt., Mar. 1946, *Jones & Onochie* FHI 16678 (BM, FHO, K), from large branch of 40 m. tree blown down by tornado, apparently from upper crown. Benin Div., Sapoba, fl., *Kennedy* 1682 (BM, FHO, K). Ife-Ilesha Div., Shasha F. R., nr. sea-level, frt., Feb. 1935, *Richards* 3040 (BM), in secondary rain-forest, tree 50 m. high, 7 m. spread, leaves glossy. Div., unknown, Ibaji-Ojoku Reserve, fl., Feb. 1934, *Taylor* L 12 (FHO). Abuja Div., Lapai, about 40 km. E. of Agaie, st., 1912, *Yates* 37 (K), tree 13–20 m. high, fringing streams.

BRITISH CAMEROONS. Victoria Div., estate by creeks of Mungo R., nr. Tiko, fl., Jan. 1926, *Dunlop* 177 (FHO), large timber tree 33–42 m. high. Id., Victoria, fl., no date or collector's name, 527 (FHO). Id., sea-level, frt. Jan. 1929, *Maitland* 232 (K), tall forest tree. Id., fl., Jan. 1898, *Preuss* 1300 (BM, EA, K, paratype), high rain-forest tree.

FRENCH CAMEROONS. Bitye, Yaunde, fl., *Bates* 19 (BM), tall tree with fine straight trunk and pale green fls. Bipindi, frt., July 1898, *Zenker* 1871 (K, lectotype; BM, isotype), rain-forest tree. Id., frt., 1903, *Zenker* 2522 (BM, K). Id., frt., 1904, *Zenker* 2944 (BM, K). Id., fl., 1911, *Zenker* 4105 (BM, K).

SPANISH GUINEA. Nkolentangan, fl., Jan. 1908, *Tessman* 111 (K), large tree.

GABOON. Nyanga, fl., July 1919, *Le Testu* 1477 (K).

BELGIAN CONGO. Bas Congo Dist., Luki on Boma-Tshela railway, fl., Dec. 1947 *Donis* 1642 (FHO), in primary forest. Ubangi Dist., Libenge on Ubangi R., frt., Nov. 1930, *Lebrun* 1686 (K). Bas Congo Dist., Temvo, on Boma-Tshela railway, frt., Feb. 1919, *Vermoesen* 1584 (FHO, K).

ANGOLA. Cabinda Dist., precise locality not given, fl., Oct. 1921, *Dawe* 205 (K), one of tallest and most conspicuous trees. Id., Mayumbe (Maiombe), frt., Jan. 1916. *Gossweiler* 6120 (BM), immense evergreen tree 27 m. high. Id., Chiluango R., fl., 1919, *Gossweiler* 6218 (BM, K).

Local uses. T. superba yields a light wood used locally in West Africa for various household purposes—match-boards, ceilings, shingles, door-frames, etc., and occasionally for canoes. It is also used locally in construction work, such as bridges. The yellow dye extracted from the bark is sometimes mixed with that from native redwoods to stain vegetable fibres.

European uses. The trade names are 'limba', 'limba noir', 'limba blanc', 'fraké', 'limbo', and 'afara'. 'Afara' and 'limba' have been recommended for use in the timber trade by the British Standards Institute (British Standard 881, p. 86 (1955)).

The wood is yellowish or olive in colour, tough, strong, of medium hardness, splits easily and works well with machine or hand tools. It is not immune to attack by termites or borers.

In Equatorial West Africa the dark walnut-brown heartwood found in certain trees is known as 'Noyer de Mayombe' or 'Congo Walnut' and is an important timber exported from the Belgian Congo. This particular wood is figured with darker striations of brown and black and is used, especially in France and Belgium, as a substitute for European walnut. It is used as a substitute for Okoumé (Olacaceae) as a veneer wood for cabinet work and panelling, and also as a substitute for imported deal.

The commoner light-coloured wood, in its best quality, is known as 'Chêne limbo' and can be used like oak. The timber from the Belgian Congo is known as 'limbo' (or 'limba') 'clair' when at least two-thirds of the diameter is light-coloured, and 'limbo' (or 'limba') 'noir' when the dark-coloured heart-wood is thick enough to show on the squared log.

Taxonomic history

T. altissima was based on *Chevalier* 16104 and 16138 both from Bouroukrou in the Ivory Coast; these specimens have not been seen, but *Chevalier* 20702! is cited, by Chevalier, as *T. altissima* (*Expl. Bot. Afr. Occ. Franç.* 1, 256 (1920)). The original description of the species shows the leaves to be somewhat larger (12–18 × 5–7 cm.) than those given for *T. superba* in Engler and Diels's monograph (8–12 × 5–6·5 cm.). Apart from the differences in measurement, which overlap to a certain extent, the description of *T. altissima* leaves no doubt that the two species are conspecific. Keay (*Fl. West Trop. Afr.* **1** (**1**), 277 (1954)) also includes *T. altissima* as a synonym of *T. superba*.

Distribution and ecology

T. superba has a discontinuous distribution throughout the rain-forest zone from French Guinea to north-western Belgian Congo, and southwards to the Cabinda District of Angola.

It is the commonest of the high forest species of *Terminalia* (24). As an invasive species it is comparatively late in making an appearance in the high forest succession. It is a typical tree of the deciduous forest zone (drier type of rain-forest), and extends into wetter high forest zones (19), usually behaving as a seral species colonizing abandoned farmland; unlike such colonizers as *Musanga cecropioides* and *Trema guineensis* which die after 30 years or so, *T. superba*, and also *Chlorophora excelsa* and *Triplochiton scleroxylon*, persist in the resulting high forest as large emergents. *T. superba* (18) is not 'aggregate' like most emergents but seems to be randomly distributed. Aggregate emergents are moderately shade tolerant but those species randomly distributed include very strong light-demanders such as *T. superba* and *Ricinodendron*, and moderate shade-bearers such as *Sterculia* spp.

It is very abundant in the deciduous forest zone in the Ivory Coast (2) and forms scattered populations with *Triplochiton scleroxylon*. It penetrates into the wetter rain-forest zone in valleys, where probably it is favoured by deforestation brought about by the local inhabitants, for it is a common species found colonizing abandoned farmland.

In Ghana (35) it occurs in the *Celtis–Triplochiton* association of Taylor, occupying areas south of the Kwahu-Mampong scarps mainly in a south-western direction. It is one of the first species to invade abandoned farmland and forms an important part of the secondary formation. It also occurs in the upper canopy of outliers of fringing forest found on higher ground with good drainage, which occur in the southern part of the Southern Guinea savannah woodland region.

Chipp (6) records *T. superba* from a number of the associations, associes and preclimax communities which he recognizes in the rain-forest regions of Ghana, but does not give much autecological information about this species.

In Nigeria (32) *T. superba* occurs in mixed rain-forest as an emergent, up to 51 m. high, in the upper storey, and is one of those deciduous forest species which are leafless for a period of weeks or months. The leafless period does not coincide with the dry season but occurs towards the end of, or even after, it. (*T. superba* and *T. ivorensis* show different phenological characteristics, the former begins to shed its leaves and fruits at the height of the dry season, whilst the latter retains its leaves and fruits until the end of the dry season and then sheds them all at once (35).) *T. superba* is one of the mixed deciduous forest species almost confined to secondary forest within the wetter rain-forest zone, probably because it is intolerant of shade (32). In the dry evergreen forest region of south-western Nigeria *Chlorophora excelsa*, *Triplochiton scleroxylon* and *T. superba* are the commonest species which colonize abandoned farmland.

T. superba is a characteristic species in *Triplochiton–Albizia* deciduous forest in the rain-forest zones of the Ivory Coast, Mayumbé and Ubangi Shari (3). In the Cameroons this community occurs just south of Nola. Aubréville points out that this drier rain-forest has been largely destroyed in this area by human activity; the regression of forest on the Cameroons plateau has probably been about 150–180 km.

In the Belgian Congo (22) the *Triplochiton scleroxylon–T. superba* association is very common in the Ubangi–Uele district between Banzyville and Yakoma. *T. superba* is also common in the *Imperata* savannah-type east of Libenge, and in the area Selenge to

Lukolela near Lake Tumba, and in gallery forest between Mushie and Bolobo, near the Kasai River south-west of Lake Léopold II. It also occurs as a characteristic species of the Mayumbé forests in the Bas Congo region (11).

In the Cabinda District of Angola (16) it is common in the forest region along the Chiluango River, and is also found in marginal forest along the Luale and Luango Rivers.

Very good natural regeneration is obtained at Sapoba; after 20 years, straight clean boles of 15–18 m. in height with a mean girth of 1·5 m. are produced. The tree will coppice from the stump. The seedlings must be lightly shaded for several months; the growth during the first two years is slow but is rapid afterwards.

(17) **T. macroptera** Guill. & Perr., *Fl. Senegamb. Tent.* **1**, 276, t. 63 (1832); Laws., *Fl. Trop. Afr.* **2**, 416 (1871); Engl. & Diels, *Monogr.* **4**, 11, t. 2 A (1900); Pobéguin, *Fl. Guinée Franç.* p. 177 (1906); Engl., *Jahrb.* **39**, 510 (1907); A. Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); Engl., *Pflanzenw. Afr.* **3** (**2**), 720 (1921); Burtt Davy & Hoyle, *Check-Lists For. Trees & Shrubs Brit. Emp.* **3** (Gold Coast), 36 (1937); Aubrév., *Fl. For. Soudano-Guinéenne*, p. 129 (1950); Eggeling & Dale, *Indigenous Trees Uganda Prot.* ed. 2, p. 90 (1951); Keay, *Fl. West. Trop. Afr.* ed. 2, **1** (**1**), 279 (1954), excl. syn. *T. chevalieri* Diels; non *T. macroptera* Mart. (1841).

T. adamauensis Engl. & Diels, *op. cit.* 11, t. 3 A; Engl., *op. cit.* 720 (1921).
T. dawei Rolfe, *J. Linn. Soc.* (*Bot.*) **37**, 516 (1906); Engl., *op. cit.* 720 (1921); Eggeling, *Indigenous Trees Uganda Prot.*, ed. 1, 47 (1940).
T. suberosa A. Chev. (non R. E. Fries), *Sudania* **1**, 121, no. 7546 (1911), nom. nud.
T. claessensii De Wild., *Pl. Bequaert.* **4**, 343 (1928), synon. nov.

See Fig. 17. Small tree, 4–10 m. high, occasionally to 12–16 m. high; bark of bole dark grey to black, rough, deeply fissured longitudinally, breaking into irregular elongated scales; slash: OB brown, IB brown with crimson markings, yellow towards inside; bark of branchlets smooth, glabrous, purplish black becoming light brown and corky with age. *Lvs.* broadly oblanceolate to narrowly or broadly elliptic-oblanceolate, apex rounded to obtuse or cuspidate or shortly acuminate, base sharply cuneate and decurrent, sessile or almost so, usually 20·8 × 7·5–26·5 × 9·3 cm., glabrous or very nearly so, undulate, thinly coriaceous, pale green; *upper surface*: midrib flattened, secondary and tertiary nerves and venation ± equally raised, nerves and venation finely pustulate, resembling strings of beads; *lower surface*: midrib prominent, secondary and tertiary nerves and venation subprominent. *Infl.* 8·5–15·5 cm. long, peduncle 1–2 cm. long, glabrous or occasionally very sparsely pilose; *fl.* glabrous; calyx-lobes acuminate. *Frt.* elliptic-oblong, apex rounded to obtuse, emarginate or style persistent, base obtuse to truncate, 9·5 × 3·5–11 × 3·8 cm., glabrous; pedicel 0·6–0·7 cm. long.

The leaves show considerable variation in size but the general shape remains fairly constant. The extreme leaf-size is about 34·5 × 13 cm. The fruits also show considerable variation in shape and size, and also in the width of the wings.

Gambia. No locality or date given, frt., *Dawe* 15 (K), small to medium-sized tree. No locality given, frt., 1866, *Ingram* s.n. (K).

Portuguese Guinea. Bissau, Bissalanca, frt., Jan. 1945, *Espírito Santo* 1640 (K), tree 4 m. high.

French Sudan. Waiguya Dist., Ouahigouya, in Yatenga tribal area, fl., frt., Aug. 1910, *Chevalier* 24798 (K).

Sierra Leone. No locality or date given, frt., *Dudgeon* s.n. (K).

Ivory Coast. Cercle de Seguela, Touba, fl., 1932, *Aubréville* 1234 (K).

Ghana. Gonja Dist., Kulmasa to Jagelo, st., Feb. 1927, *Kitson* 531 (K). Dist. unknown, Sa (?Wa), frt., Mar. 1927, *Kitson* 845 (K). Wa Dist., Bele to Sombisi, st., May 1927, *Kitson* 959 (K). Mamprusi Dist., Nasia, alt. 160 m., frt., July 1934, *Vigne* 3300

(FHO), very common in Nasia swamp, forming over 70% stocking in parts; tree 6 m. high, 0·6 m. girth.

Togo. Sokode, fl., 1905, *Kersting* 5 (BM.) Atakpame, frt., Nov. 1913, *Mildbraed* 7456 (K).

Nigeria. Kontagora Div., Kontagora, fl., Feb. 1906, *Dalziel* 284 (K), tree in the bush. Egba Div., Olokemeji F. R., st., Jan. 1946, *Keay* FHI 14607 (K), in open savannah woodland with *Anogeissus*, *Crossopteryx*, *Terminalia glaucescens* and *Pseudocedrela*; tree 8 m. high, 0·25 m. girth, bark grey, deeply fissured longitudinally, flaking; slash: OB 8 mm., brown, IB 10 mm., crimson changing to yellow of inner 6 mm., sapwood dry, pale straw colour. Oyo Div., Old Oyo F. R. in Old Oyo (deserted about 1840), fl., Feb. 1946, *Keay* FHI 16015 (BM, FHO), tree 10 m. high with spreading crown and apple-green leaves. Sokoto Div., Sokoto, alt. 500 m., frt., May 1923, *Lely* 818 (K), large tree in clumps or gregarious over large areas; bark black, leaves large, smooth, pale green. Zaria Div.,

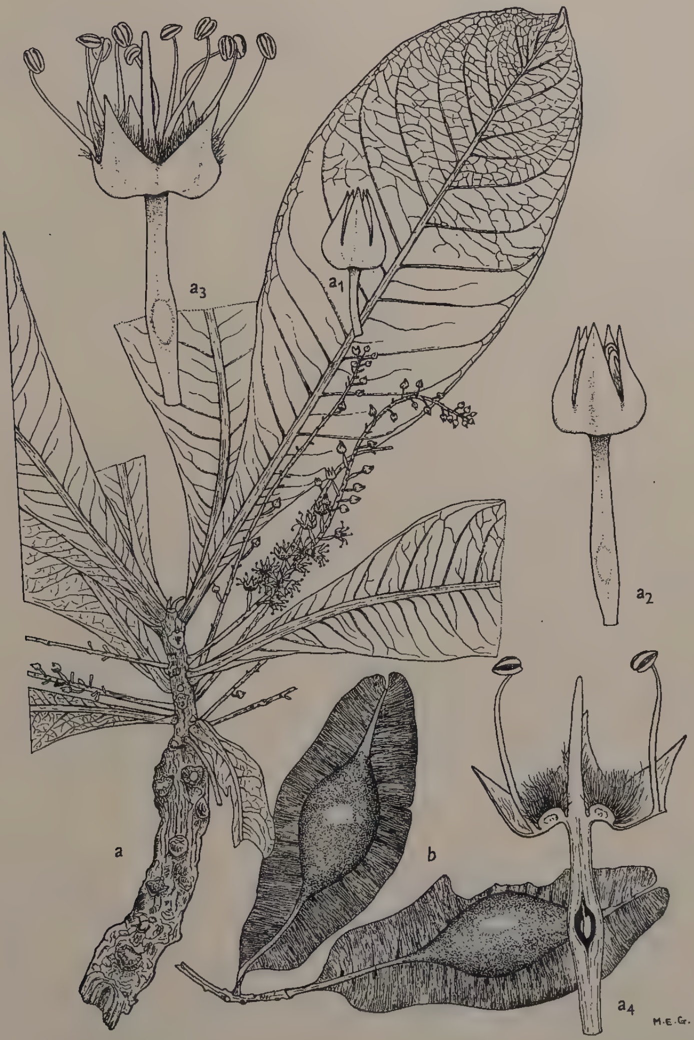

Fig. 17. *T. macroptera* Guill. & Perr. *a*, from *Hoyle* 477; a_1–a_4, from *Chandler* 624; *b*, from *Vigne* 3300.

Zaria, fl., Mar. 1927, *Unwin* 32 (FHO), medium-sized tree of open savannah, often gregarious.

UBANGI-SHARI. Dar Kuti Occidental, Ndele, fl., frt., Feb. 1903, *Chevalier* 7546 (P), rather rare on the plains; shrub or tree 5–8 m. high with twisted trunk and thick corky bark. Moyen Logone, Kongola to Buar, summer 1914, *Mildbraed* 9120 (BM, K), with galled infls, 50–60 km. S.E. of Buar, alt. 800 m., frt., June 1914, *Mildbraed* 9631 (K).

BELGIAN CONGO. Kibali Ituri Dist., Aru, frt., Sept. 1921, *Claessens* 1540 (BR, holotype of *T. claessensii*).

SUDAN REPUBLIC. Equatoria Prov., nr. Ndongo (or Besi) N.W. of Said Bundus, fl., Jan. 1939, *Hoyle* 477 (BM, FHO), scattered in *Isoberlinia* woodland, dominant in damper areas; tree 8–16 m. high; bark dark grey, longitudinally ridged, dividing into elongated irregular scales; slash: OB pinkish brown to crimson, IB lemon yellow; sapwood deep yellow; leaves pale apple green, fleshy, waxy. Id., 12–16 km. from Wau on Wau–Meshra'er Req Rd., frt., Feb. 1939, *Hoyle* 581 (FHO), most frequent species in 'edge-of toich' *Terminalia* zone, associated here, at its upper edge, with *T. laxiflora* and *Nauclea esculenta*. Id., Loka, alt. 1000 m., frt., June 1952, *Jackson* 2263 (FHO), characteristic tree of illuvial zone with impeded drainage but found occasionally elsewhere; tree 10 m. high, 30 cm., dbh., bole 2·5 m. long; bark rough, dark grey, scales 15 × 5 cm., separated by irregular fissures 1·7 cm. wide, 1·2 cm. deep; slash: OB 1·2 cm., with alternate layers of pale brown and dark cinnamon, IB dull beefy red, fibrous, grading into yellow; sapwood bright yellow; frt. bright purplish red. Blue Nile Prov., Fazokel (= Fazogli), frt., *Kotschy* 536 (K, OXF). Equatoria Prov., Lado, Yei R., frt., Nov. 1919, *Sillitoe* 155 (K), tree 10 m. high with red frt.

UGANDA. Teso Dist., Serere, alt. 1200 m. fl., frt., Feb. 1933, *Chandler* 624 (EA, FHO, K), in uncleared bushland, medium-sized tree 7–8 m. high, fls. yellow with strong rather unpleasant aroma. Acholi Dist., Acholi, frt., 1905, *Dawe* 865 (K, holotype of *T. dawei*), small tree. Id., 16 km. W. of stream nr. northern boundary of Abera Forest Station, 12 km. from Gulu on Kitgum Rd., alt. 1160 m., frt., Feb. 1947, *Dawkins* 239 (FHO), on slight eastern slope, on brown loam in annually burnt *Imperata* regrowth from cultivation, coarsely branched tree up to 8 m. high, bark grey, coarsely longitudinally fissured, brittle, rusty at bottom of fissures, young leaves shiny, faint reddish tinge especially distally. West Nile Dist., E. Madi nr. Obongi, alt. 800 m., frt., June 1933, *Eggeling* 1238 (K), tree 13 m. high, bark blackish brown, foliage dense, leaves large, glaucous-green, glabrous, midrib white, distinct on both surfaces. Lango Dist., Nabieso, Kwania country, frt., Sept. 1935, *Eggeling* 2198 (FHO).

Taxonomic history

T. macroptera was based on fruiting specimens collected by Perrottet at Albreda in Gambia; although these have not been seen, the species known under this name agrees with the original description and illustration.

T. adamauensis was based on *Passarge* 109 (fl.) from the Adamaoua region of the Cameroons; the type has not been seen, but the description and illustration in Engler & Diels's monograph reveal no characters which can be used to separate it from *T. macroptera*.

T. dawei was based on *Dawe* 865! (frt.) from Acholi country in Uganda, and only differs in the somewhat larger leaves and in the lamina (always decurrent to the base of the petiole), which is rather broader than usual at this point.

The type specimen of *T. suberosa* is *Chevalier* 7546! (frt.) from Ndele in Ubangi Shari, listed in *Sudania*, **1**, 121 (1911); it is a nomen nudum. Its fruits are longer and narrower than usual, but come within the range of variation for *T. macroptera*.

T. claessensii was based on *Claessens* 1540! (frt.) from Aru in north-eastern Belgian Congo; it is certainly conspecific with *T. macroptera*.

Distribution and ecology

T. macroptera is distributed from Gambia to the Blue Nile Province of the Sudan Republic, penetrating further south to Southern Uganda; its northern limit is in the Waiguya district of French Sudan.

In the Northern Guinea Zone of Nigeria (21) the open woodland of *T. macroptera* with tall dense grass is a striking community characteristic of the heavier, relatively poorly drained soils, either among rocky hills at the sources of streams or lower down the catena above the flood plain. In this zone (20) it occupies sites similar to those occupied by almost pure stands of *Acacia seyal* in the Sudan zone, and forms pure, open savannah woodland in low-lying riverain sites and in depressions at the sources of small streams. In the Southern Guinea zone in Nigeria (19) on low-lying ground such as flood plains with heavy clay soils, the grass is tall and dense, and only widely spaced trees of a specialized type are found; *T. macroptera*, *T. glaucescens* and *Mitragyna inermis* are three such species.

In the Cameroons (4) *T. macroptera* occurs gregariously on wet ground or on ground periodically flooded. On the high ground of the Adamaoua Plateau it occurs with *T. mollis* and is an abundant and characteristic tree of the savannah woodland of this area. It is one of the six principal species in this dry savannah type (3); the other species are *Daniellia oliveri*, *Lophira lanceolata*, *Syzygium guineense* var. *macrocarpa*, *T. mollis* and *Pithicellobium eriorachis*. This type occupies the region above the *Isoberlinia–Uapaca–Monotes* woodland occurring on the steep slopes of Adamaoua Plateau. Between Ngaoundéré and Tibati (3) patches of low dry forest exist which have a closed and primitive aspect, and are not fired. These patches include a mixture of the neighbouring savannah woodland species and those species of a wetter type of woodland normally not frequently found in an isolated state in savannah; *T. macroptera* and *T. mollis* belong to the latter type, *T. glaucescens* to both.

In Ubangi Shari (3) *T. macroptera* occurs in the dry *Anogeissus* forest of the Ouanda Djalé Mt. region, in the colluvial zone on the scree slopes or towards the foot of the mountain. An edaphic savannah occurs in areas periodically flooded; these marshy plains, which have a cracked clay surface during the dry season, extend over a vast area of the Tchad Colony, at Baquirmi in particular. Large areas also occur in Ubangi-Shari in the Logone valley and in the Fort Archambault area. That part of the Northern Cameroons which touches the southern shore of Lake Tchad forms part of the great flood zone of Lake Tchad and the Chari delta. Almost pure populations of *T. macroptera*, with some *Lophira* and *T. laxiflora*, occur in these areas.

In the Sudan Republic (28) *T. macroptera* and *T. laxiflora* are two of the dominant trees in the drained upper parts of the illuvial zone, where alternation of flooding and effective drainage exists. As this type of site occurs at the edge of grazing lands of pure grasslands that are fired every year, the plants are subjected to a very powerful fire selection. The three catenas studied by Morison, Hoyle and Hope-Simpson were at Halima (upper parts of main tributary river), Wau (lower parts of tributary river), and Aweil (flood-plain region); all in the Equatoria Province. *T. macroptera* occurred in all three stations.

In the Karamoja district of Uganda (12) it is common with *T. glaucescens* and *T. mollis* on alluvial soils in the *Combretum*–other species open woodland.

Its other localities in Uganda, and the localities in the Kibali Ituri district of the Belgian Congo come within the region of lower-montane derived savannah with remnants of rain-forest which occurs over most of Uganda, and, in the Belgian Congo, borders on the large rain-forest area.

(18) **T. laxiflora** Engl. in Engl. & Diels, *Monogr.* **4**, 12, t. 2 B (1900); Engl., *Jahrb.* **39**, 510 (1907); A. Chev., *Études Fl. Afr. Centr. Franç.* **1**, 119 (1913); A. Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); Engl., *Pflanzenw. Afr.* **3** (2), 720 (1921); Aubrév., *Fl. For. Soudano-Guinéenne*, p. 131 (1950); Keay, *Fl. West Trop. Afr.* ed. 2, **1** (1), 279 (1954).

T. elliotii Engl. & Diels, *op. cit.* 12, t. 3 B (1900); Engl., *op. cit.* 720 (1921).
T. schweinfurthii Engl. & Diels, *op. cit.* 12 (1900); Engl., *op. cit.* 720 (1921).
T. chevalieri Diels, Engl., *Jahrb.* 510 (1907); A. Chev., *Bull. Soc. Bot. Franç.* **54**, *Mém.* **8**, 21 (1907); A. Chev., *op. cit.* 256 (1920); Engl., *op. cit.* 720 (1921).
T. sokodensis Engl., *op. cit.* 510 (1907); Engl., *op. cit.* 720 (1921); Burtt Davy & Hoyle, *Check-Lists For. Trees Shrubs Brit. Emp.*, **3** (Gold Coast), 36 (1937).
T. repanda A. Chev., *Sudania*, **1**, 121, no. 7547 (1911), nom. nud.; A. Chev., *op. cit.*, 119 (1913), nom. nud.; Engl., *op. cit.* 720 (1921), nom. nud.
Terminalia sp. aff. *schweinfurthii* Engl. & Diels, Eggeling & Dale, *Indigenous Trees Uganda Prot.*, ed. 2, p. 94 (1951).

See Fig. 18. Small tree, 3–10 m. high, occasionally to 13–16 m. high; bark of bole dark grey, thick, rough, ridged and deeply fissured longitudinally; slash red; bark of branchlets purplish brown, smooth, glabrous (except in pubescent forms), becoming light brown and corky with age. *Lvs.* elliptic, elliptic-oblong or broadly oblanceolate, apex rounded to obtuse or shortly acuminate, base obtuse to cuneate, (13·5 × 4·5 –) 16–22 (– 30) × 9·5 cm., glabrous, or tomentose on midrib above and main nerves beneath (more rarely tomentose ± all over lower surface), finely undulate, subcoriaceous, pale green; *upper surface*: midrib and secondary nerves flattened or slightly impressed, tertiary nerves and venation raised and finely pustulate resembling strings of beads; *lower surface*: midrib and secondary nerves prominent, tertiary nerves not prominent, venation obscurely reticulate; petiole 2·8–3·4 cm. long. *Infl.* 9–12·3 cm. long, peduncle 1·7–2·2 cm. long, glabrous or sparsely to densely tomentose; *fl.*: lower receptacle glabrous or sparsely to densely tomentose, upper receptacle glabrous or sparsely pilose at base; calyx-lobes acute. *Frt.* oblong to oblong-elliptic, apex obtuse to rounded, style frequently persistent, base obtuse to subacute, 5·7 × 2·6–8 × 3·5 cm., glabrous, at least when mature; pedicel 1–1·2 cm. long.

T. laxiflora is a very variable species showing considerable variation in the size and shape of the leaves and the fruits, the amount of indumentum on the leaves and branchlets and on the inflorescence.

PORTUGUESE GUINEA. No locality or date given, fl., frt., *Espírito Santo* 520 (K).

SIERRA LEONE. Koinadugu Dist., 2 km. W. of Falaba, on Musaia–Falaba Rd., fl., Apr. 1951, *Deighton* 5402 (K), single group in orchard-bush savannah, tree 5–7 m. high., fls. with unpleasant scent, white. Id., Musaia, frt., Apr. 1951, *Deighton* 5486 (K), in dense orchard-bush savannah, tree 10 m. high with rugged bark. Dist. unknown, Erimakuna, fl., Mar. 1892, *Scott-Elliot* 5200 (BM, K, isotype of *T. elliotii*), common on laterite plateau, tree about 7 m. high.

IVORY COAST. Bobo Dioulasso, frt., *Aubréville* 1979 (K).

GHANA. Dagomba Dist., between Yendi and Demon, frt., May 1936, *Akpabla* 550 (K), tree, usually seen in swampy places in savannah woodland. Wenchi-Sunyani Dist., Weila, alt. 340 m., fl., Apr. 1934, *Kinloch* 3274 (FHO, K), medium-sized tree of savannah woodland, common around Weila. Dagomba Dist., nr. Karaga, fl., Apr. 1928, *Lloyd Williams* 151 (K), in savannah, tree 8 m. high, branching high up, bark with large crumbling scales, dark grey, slash red, fls. with unpleasant scent, white. Gonja Dist., Grube, fl., Mar. 1929, *Rea* 1670 (BM, FHO). Mamprusi Dist., Zuarungu, frt., June 1938, *Vigne* 4574 (BM), in savannah woodland, tree 10 m. high, 1·2 m. girth.

NIGERIA. Adamawa Div., Yola, fl., frt., May 1909, *Dalziel* 91 (K), large tree. Udi Div., Enugu, fl., *A. P. D. Jones* FHI 1122 (K). Oyo Div., about 3 km. beyond western boundary of Olokemeji F. R., fl., Mar. 1948, *Keay & Foggie* FHI 22534 (BM, K), in open savannah on diorite-derived black clay soil, with *Pseudocedrela, Combretum sokodense* and *Vitex doniana*; tree 12 m. high, bark fissured, black, leaves pale glaucous green, young leaves and stems purplish. Bauchi Div., Bauchi Plateau, fl., frt., *Lely* 854 (K). Katsina Div., Dan Ja, frt., May 1946, *McElderry* FHI 16484 (BM), in savannah on old farm land, very common, small tree 2–3 m. high.

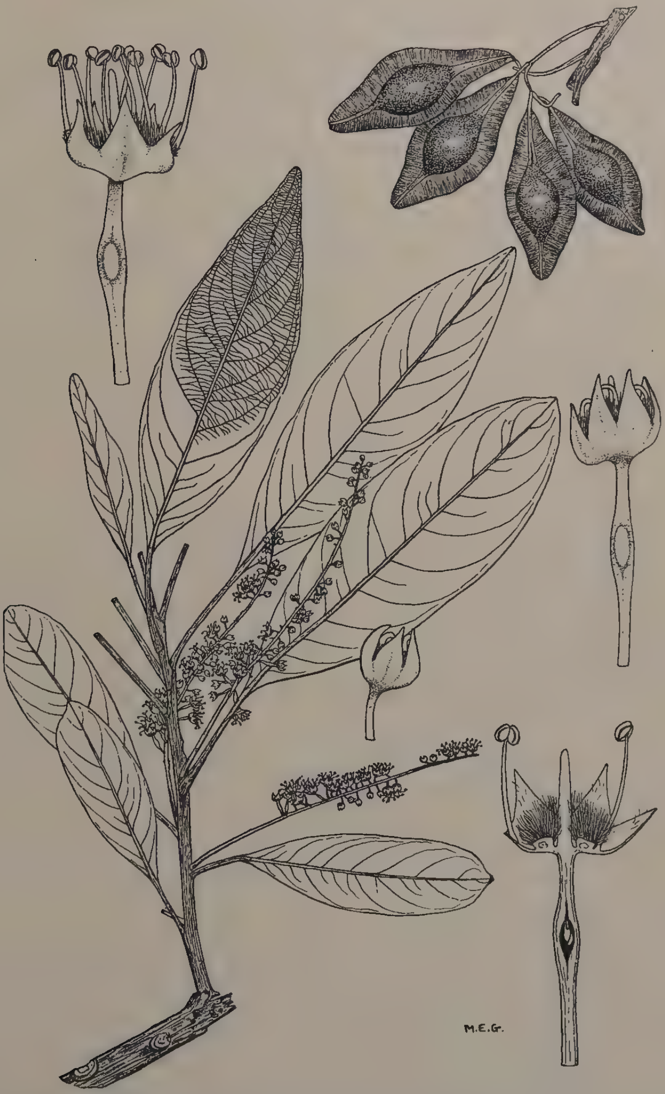

Fig. 18. *T. laxiflora* Engl. in Engl. & Diels. Flowering specimen from *Keay & Foggie* FHI 22534. Fruiting specimen from *Akpabla* 550.

TCHAD. Da, nr. Lake Tchad, fl., June 1899, *Chevalier* 1017 (P, holotype of *T. chevalieri*), in savannah, tree 5–6 m. high, with thick corky bark and white fls.

UBANGI-SHARI. Dar Kuti Occidental, Ndele, frt., Feb. 1903, *Chevalier* 7547 (P), extremely abundant in this area, shrub or tree 3–8 m. high, leaves vary variable, velutinous or glabrous when young. Moyen Logone, Zinchen Plateau nr. Nana R., at Buar, alt. 1000 m., frt., May 1914, *Mildbraed* 9310 (K). Buar, alt. about 1000 m., frt., July 1914, *Mildbraed* 9801, 9802 (K).

British Cameroons. Bamenda Div., Furu, alt. 1400 m., fl., Feb. 1931, *Johnstone* 39/31 (FHO), in orchard-bush, small tree.

French Cameroons. Between Sansane and Kongola, alt. 750–800 m., st., Apr. 1914, *Mildbraed* 8983 (K). Ngaoundéré, Mbussa on Lom R., alt. 800–900 m., frt., Apr. 1914, *Mildbraed* 9163 (K).

Sudan Republic. Kordofan Prov., 65 km. W. of El Odaiya, alt. 500 m., frt., Nov. 1954, *Jackson* 3250 (FHO), common, and in places dominant on sandy areas of Kordofan with more than 500 mm. rainfall; tree 8 m. high, 0·3 m. diam., bark deeply fissured with thick corky ridges. Equatoria Prov., Grosse Seriba Ghattas (=Tonj), in Jurland, fl., Apr. 1869, *Schweinfurth* 1336 (BM, K, paratype of *T. laxiflora*). Id., frt., July 1869, *Schweinfurth* 2088 (BM, isotype; K, lectotype). Blue Nile Prov., Gallabat, on left bank of Gendua R., young frt., June 1865, *Schweinfurth* 2120 (BM, K, syntype of *T. schweinfurthii*), large tree. Same locality, st., young frt., June 1862, *Steudner* 195, 205 (K, syntypes of *T. schweinfurthii*).

Uganda. West Nile Dist., Leya R., watershed, alt. 1800 m., fl., Mar. 1945, *Greenway & Eggeling* 7249 (EA), common, but scattered, on stony hill slopes in *Lophira alata–Butyrospermum–Hymenocardia–Crossopteryx* wooded grassland; laxly branched tree up to 7 m. high, bark longitudinally fissured, corky, greyish black, fls. greenish white.

Taxonomic history

T. elliotii was based on *Scott Elliot* 5200! (fl.) from Sierra Leone. Leaves 10–15 × 4–5 cm., oblong; they are slightly narrower than typical *T. laxiflora* (15–25 × 6–15 cm., obovate to broadly elliptic). The measurements are taken from the original description. *T. elliotii* comes within the range of variation of *T. laxiflora*, which shows considerable variation in the size and shape of the leaves.

T. schweinfurthii was based on *Steudner* 195! (st.) and 205! (young frt.) from Gallabat on the boundary between the Sudan Republic and Ethiopia, and *Schweinfurth* 2120! (young frt.) and 2121 (frt.) from the same locality. *T. schweinfurthii* differs from the type material of *T. laxiflora* in having much larger, broader leaves (15–30 × 10–15 cm.); the fruits are almost the same size. *T. schweinfurthii*, however, comes within the range of variation of *T. laxiflora*.

T. chevalieri was based on *Chevalier* 1017! (fl.), from the Lake Tchad area; lvs. 10–15 × 2·5–5 cm.; the leaves are narrower than usual; but match some of the material of *T. laxiflora* from Nigeria.

T. sokodensis was based on *Kersting* 473 (frt.) from Togo; lvs. 15–18 × 4·5–5·5 cm. The fruits are rather smaller than usual—4·5 × 1·5–2 cm. The type has not been seen, but there is nothing in the description to separate it from *T. laxiflora*.

T. repanda based on *Chevalier* 7547! (frt.) is a nomen nudum; the leaves (about 24 × 8 cm.) are rather larger than most of the material of *T. laxiflora*, but it is undoubtedly conspecific with the latter species.

T. salicifolia Schweinf., *Verh. Zool.-Bot. Ges. Wien*, 18, 663 (1868), is doubtfully distinct from *T. laxiflora*; it was based on *Schweinfurth* 2127! (fl.) from Ethiopia, and differs from *T. laxiflora* only in the very much narrower leaves (12–19 × 3–4 cm.). For the present, it is regarded as an imperfectly known species, as the author has not had an opportunity of examining other material from Ethiopia.

Hutchinson and Dalziel (*Fl. West Trop. Afr.* **1**, 226 (1927)) maintain *T. sokodensis* as a separate species and include *T. elliotii* as a synonym of *T. macroptera*. Keay (*op. cit.* ed. 2) brings the synonymy up to date and includes *T. sokodensis* and *T. elliotii* as synonyms of *T. laxiflora*. In both editions *T. chevalieri* is placed as a synonym of *T. macroptera*, but from the type specimen it is obvious that it is a synonym of *T. laxiflora*. Aubréville (*Fl. For. Soudano-Guinéenne*, 131 (1950)) includes *T. schweinfurthii* and *T. repanda* as synonyms of *T. laxiflora*, a view which is followed here. These two species are not West African.

Distribution and ecology

T. laxiflora extends from Portuguese Guinea to the Blue Nile Province of the Sudan Republic, with its northern limit around Lake Tchad and its southern limit in the West Nile District of Uganda.

It is very abundant in the Upper Volta area (4) in the Bobo Dioulasso–Dédougou–Boromo region, and it is also found in parts of French West Africa, such as Bamako in the French Sudan, Katiola in the Ivory Coast, and Fada N'gourma in the Niger Colony. It invades cleared forest areas, e.g. on the sandstone cliffs of Banfora in the Ivory Coast, and on rocky hills in Togoland.

In Ghana and Nigeria it has a similar distribution to that of *T. macroptera*, and occurs in the Guinea and Sudan Zones.

In the Cameroons (4) it does not occur in the savannah woodland of the Adamaoua Plateau, unlike *T. macroptera* and *T. mollis*. However, it does occur in Ngaoundéré region farther south.

In Ubangi Shari (4) it is very common in the Shari Basin and on the Bocaranga Massif. It occurs in the dry forest of Leguminosae and *Anogeissus* (3) which dominates large areas of the Logone-Chari region and in the Haute Kotto region in the east. It is one of the species which follow *T. glaucescens*, *Parkia clappertoniana* and other pioneer species in the sucession colonizing abandoned farmland. It accompanies *T. macroptera* in the large flood area of Lake Tchad and the Chari delta (see under *T. macroptera*, p. 867).

In the Sudan Republic (28) it occurred with *T. macroptera* as one of the dominant trees in the drained upper parts of the illuvial zone at Halima and Wau. At Wau it was found in the colluvial-illuvial transition zones between the *Combretum* scrub and *Terminalia* woodland, and also occurred as an occasional subcanopy tree and as saplings or coppice in the *Combretum* scrub, and was frequent to locally dominant in the *Terminalia* woodland.

(19) **T. mollis** Laws., *Fl. Trop. Afr.* **2**, 417 (1871); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, **2**, 145 (1954); Keay, *Fl. West Trop. Afr.* ed. 2, **1** (**1**), 279 (1954); non *T. mollis* Zoll. ex Teysm. & Binn. (1866) nomen, nec Zoll. ex v. Sl. (1924) descr. nec (Presl) Vidal (1885).

T. torulosa F. Hoffm., *Beitr. Kenntn. Fl. Centr. Ost.-Afr.* p. 27 (1889); Engl., *Pflanzenw. Ost.-Afr.* C, 294 (1895); Engl. & Diels, *Monogr.* **4**, 15, t. 5 (1900) excl. *Kirk* s.n.; Engl., *Jahrb.* **39**, 512 (1907); A. Chev., *Études Fl. Afr. Centr. Franç.* **1**, 119 (1913); A Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); Engl., *Pflanzenw. Afr.* **3** (**2**), 722 (1921); Eggeling & Dale, *Indigenous Trees Uganda Prot.* ed. 2, 93 (1951).

T. dewevrei De Wild. & Th. Dur., *Bull. Soc. Roy. Bot. Belge*, **38**, 123 (1899); De Wild. & Dur., *Ann. Mus. Cong.*, *Bot.*, sér., **3**, Reliq. Dewevr., fasc. **2**, 84 (1901); Th. & H. Dur., *Syll. Fl. Cong.* 195 (1909); Aubrév., *Fl. For. Soudano-Guinéenne*, p. 132 (1950), synon. nov.

T. spekei Rolfe, *J. Linn. Soc.* (*Bot.*), **37**, 516 (1906); Engl., *op. cit.* 722 (1921); Eggeling, *Indigenous Trees Uganda Prot.*, ed. 1, 47 (1940).

T. kerstingii Engl., *op. cit.* 511 (1907); Engl., *op. cit.* 721 (1921).

T. reticulata Engl., *op. cit.* 511 (1907); Engl., *op. cit.* 721 (1921); Burtt Davy & Hoyle, *Check-Lists For. Trees & Shrubs Brit. Emp.*, **3** (Gold Coast), 36 (1937); Aubrév., *op. cit.* 132; non *T. reticulata* Roth (1821).

T. suberosa R. E. Fries, *Wiss. Ergebn. Schwed. Rhod.-Kongo Exped.* 1911–12, **1**, 172, t. 4 (1914); Engl., *op. cit.* 722 (1921), synon. nov.; non *T. suberosa* A. Chev.

T. glandulosa De Wild., *Contrib. Fl. Katanga*, suppl. **2**, 86 (1929).

Terminalia sp. cf. *mollis*, Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr.), **2**, 144 (1949).

See Fig. 19. Small tree, 5–13 m. high, occasionally to 16–20 m. high; bark of bole blackish grey, thick, much fissured longitudinally; slash red; bark of branchlets light grey-brown, densely tomentose, becoming dark grey-brown, glabrous, and corky with age. *Lvs.* elliptic to obovate-oblong, apex obtuse to rounded, occasionally acute, base obtuse to rounded, occasionally subcordate, 16 × 7–32 × 11 cm., densely tomentose on midrib and secondary nerves on both surfaces, pubescent to tomentose on tertiary nerves, veins and lamina beneath, subcoriaceous; *upper surface*: midrib flattened or with central

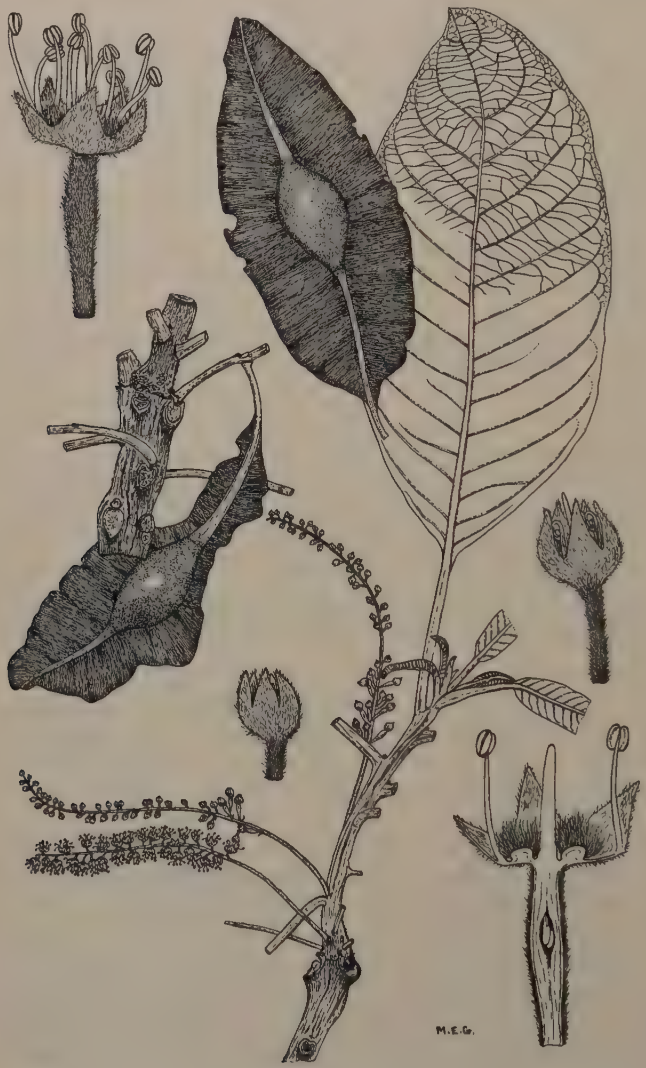

Fig. 19. *T. mollis* Laws. Flowering specimen from *Holmes* 892. Fruiting specimen from *White* 3623.

furrow, secondary and tertiary nerves and venation ± impressed or obscurely raised, tertiary nerves and venation obscurely papillose; *lower surface*: midrib and secondary nerves prominent, tertiary nerves and venation prominent or subprominent; petiole 3·5–5 cm. long. *Infl.* 8–17 cm. long, peduncle 1–2 cm. long, densely tomentose; *fl.*: lower receptacle densely tomentose, upper receptacle sparsely tomentose, ± glabrous towards calyx-lobes; calyx-lobes acute. *Frt.* oblong to broadly elliptic, apex obtuse to rounded, emarginate or style persistent, base acute to subtruncate, 6·5 × 2·8–11·5 × 5·5 cm., densely velutinous-tomentose; pedicel 0·5–0·7 cm. long.

The leaves show considerable variation in size, mostly ranging from 16 × 7 cm. to 31·5 × 11 cm. but, on the whole, the general shape of the leaves remains fairly constant. Material from West Africa is poorly represented in European herbaria, and most of the specimens consist of only detached leaves and fruits; the leaves are rather broader than usual—32 × 15 cm. The fruits are very variable; the two extremes of size are in the region of 6·5 × 2·8 and 12·5 × 6 cm., the width of the wings also varies; the shape varies from oblong to broadly elliptic.

GHANA. Dogomba Dist., Lungbungu to Sambu, st., May 1927, *Kitson* 726 (K). Birim Dist., Dedesu to Nurubong, Afram Plains, frt., May 1928, *Kitson* 1133 (K), small tree, straggling branches, bark thick, coarsely ribbed, black and dark grey. Id., Abetifi to Kwahu, frt., June 1908, *Thompson* 85 (K). Gonja Dist., Yeji, alt. 140 m., frt., July 1926, *Vigne* 1226 (FHO), common in parts of savannah woodland; small tree up to 6 m. high, 0·6 m. girth, leaves large. Dagomba Dist., Yendi, alt. 240 m., fl., Apr. 1929, *Vigne* 1690 (FHO), in savannah woodland, tree 5 m. high, leaves very velvety when young, frt. large.

TOGO. No locality or date given, frt., *Kersting* A 196 (K).

UBANGI-SHARI. Dar Kuti Occidental, Golo, frt., Mar. 1903, *Chevalier* 7763 (K), very common on ferrugineous soil between Golo and Dialmada. Ndele, frt., Apr. 1903, *Chevalier* 8173 (K). Moyen Logone, Buar, alt. about 1100 m., frt., June 1914, *Mildbraed* 9561 (BM, K).

FRENCH CAMEROONS. Ngaoundéré, Kongola, alt. 750–800 m., frt., Apr. 1914, *Mildbraed* 8997 (BM, K).

BELGIAN CONGO. Tanganyika Dist., Kimaunga to Lukulu, frt., Oct. 1921, *Delevoy* 487 (BR, syntype of *T. glandulosa*). No locality or date given, frt., *Dewevre* s.n. (BR, holotype of *T. dewevrei*), bushy tree 8–9 m. high with large leaves and greenish yellow frt. Kwango Dist., Dembo de la Kampemba, nr. the Arboretum extension, alt. about 1200 m., fl., Oct. 1927, *Ritschard* 1506 (BR, syntype of *T. glandulosa*), on grey-yellow soil, gravelly in places, tree 10 m. high, trunk 4 m. high, 0·2–0·3 m., diam., branches irregular, stout, black, bark very rough, grey-black, upper parts falling to expose brown surface, specimen coll. from middle of crown. Haut Katanga Dist., Keyberg Station, 8 km. S. of Elizabethville, fl., Oct. 1948, *Schmitz* 2062 (BR), in savannah at edge of river, flooded in rainy season, tree with rounded crown. Uele Dist., Garamba National Park, 27 km. from Congo border, alt. 800–900 m., fl., Nov. 1952, *Troupin* 34 (BR), in savannah woodland, tree 3–4 m. high with white fls.

SUDAN REPUBLIC. Equatoria Prov., nr. Loa Resthouse, 32 km. N. of Nimule, frt., Apr. 1948, *Jackson* 293 (FHO), in annually burnt savannah, with *Combretum binderanum C. ghasalense*, *Pseudocedrela*; small gnarled tree with dark grey, ridged bark. Dist. unknown, Nileland (probably near Tonj), fl., *Petherick* s.n. (K, holotype). Equatoria Prov., Yambio-Maridi Rd., fl., frt., Jan. 1937, *Ruttledge* 29 (K), small to medium-sized tree with spreading, rather sinuous branches, bark deeply fissured longitudinally, lightish-grey, leaves large, in terminal tufts except on green wood; just coming into new leaf and fl. Id., Grosse Seriba Ghattas (=Tonj) in Jurland, frt., Apr. 1869, *Schweinfurth* 60, 1786 (K).

RUANDA URUNDI. Kagera National Park, Mt. Lutare, alt. 1600 m., frt., Jan. 1938, *Lebrun* 9585 (BR, K), in savannah woodland, small tree to 6 m. high, bark fissured, whitish grey, frt. yellowish green.

UGANDA. Teso Dist., Serere, alt. 1200 m., fl., Feb. 1932, *Chandler* 625 (EA, FHO, K), in uncleared bushland, medium-sized tree 7–8 m. high, fls. with unpleasant scent, pale yellow. Acholi Dist., Acholi country, alt. 1200 m., fl., frt., *Dawe* 858 (K, syntype of *T. spekei*), small tree 3–7 m. high. Mengo Dist., on rocky hillside nr. Bukomero, about 32 km. N. of Mityana, fl., Aug. 1932, *Eggeling* 489 (K), in open bush, with *Strychnos*, *Hymenocardia* and *Combretum*; small tree, 8–10 m. high, with light greenish yellow fls. Karamoja Dist., between Amaler and Napyenenya, at foot of Mt. Debasien, fl., frt., Jan. 1936, *Eggeling* 2577 (EA, K), tree to 10 m. high. West Nile Dist., woods of Madi, frt., Dec. 1862, *Speke & Grant* 643 (K, syntype of *T. spekei*).

KENYA. Trans-Nzoia Dist., Kitale, alt. 2070 m., frt., Sept. 1952, *Bogdan* 3588 (EA, K), co-dominant tree in *Combretum* savannah. N. Kavirondo Dist., Bunkura Mt., alt. 1300 m., fl., Mar. 1944, *Graham* 61 (EA, FHO, K), savannah tree to 7 m. high, bark rough, corky, fls. with strong unpleasant scent, greenish white. Id., nr. Bungoma, alt. 1570 m., frt., July 1915, *Greenway & Doughty* 8530 (EA, FHO, K), a common dominant with *Combretum* sp., *Acacia* spp., *Entada*, *Bauhinia*, *Hymenocardia* and *Cassia singueana* in native cultivations in a *Themeda–Hyparrhenia–Cymbopogon* grassland; open branched tree with short bole and rounded crown, bark fissured, dark grey to black, leaves dark green above, densely grey-pubescent beneath. Trans-Nzoia Dist., Mt. Elgon, alt. 2160 m., fl., *T. Jackson* 373 (K), tree 16–20 m. high, fls. white. Id., about 24 km. N. of Kitale, frt., July 1938, *Pole Evans & Erens* 1498 (K), tree 5 m. high, growing in grassveld.

TANGANYIKA TERRITORY. Singida Dist., Mkalama, alt. 1830 m., fl., Oct. 1935, *Burtt* 5241 (FHO). Kahama Dist., Mkwemi, nr. Kahama, alt. 1330 m., frt., Feb. 1937, *Burtt* 5480 (K), locally common, in clay soil valleys in *Brachystegia* woodland, tree 3–8 m. high. Tabora Dist., Ugalla R. area, Kakoma-Ugalla Rd., frt., June 1949, *Hoyle* 1036 (FHO), tree, bark deeply fissured, dark grey, OB brown, dry, laminated, IB brownish yellow, grading to bright greenish golden-yellow, shortly fibrous, very moist. Mpanda Dist., Nyonga–Ilunde–Rungwa Rd., 6 km. E. of Nyonga, frt., July 1949, *Hoyle* 1065 (FHO), small tree, bark of 'expanded-metal' type, pale grey, OB streaked dark and light brown, IB 2-layered, outer reddish brown, inner cinnamon-yellow, sapwood bright yellow. Bukoba Dist., 112 km. S. of Bukoba on the Biharamulo Rd., alt. 1333 m., fl., Aug. 1952, *Proctor* 85 (EA, K), growing on poor murram soil, with outcrops of Bukoba sandstone, small tree to 7 m. high.

NORTHERN RHODESIA. Mazabuka Dist., on Native Trust Land adjoining Great North Rd., N.E. of Pemba, frt., Mar. 1952, *Cooling* 40 (FHO), growing at edge of dambo in *Brachystegia* woodland; tree 8 m. high with very thick, rough, grey and brown bark. Broken Hill Dist., Chirukutu, nr. Broken Hill, st., Aug. 1911, *Fries* 264 (UPS, syntype of *T. suberosa*); same locality and date, frt., *Fries* 264 a (UPS, syntype of *T. suberosa*). Mwinilunga Dist., on Zambezi, 6 km. N.W. of Kalene Hill Mission Station, fl., Sept. 1952, *Holmes* 892 (FHO), on detrital soil derived from granite, small tree 8 m. high, 0·9 m. girth, bark peeling in flakes on 2nd year branches, bark of trunk thick, with deep interlaced vertical fissures, OB light grey passing through red-brown to dark straw-yellow. Kasama Dist., 48 km. S. of Kasama, at Forest Camp on bank of Lukulu R., where it flows nearest to Kasama–Mpika Rd., fl., Oct. 1949, *Hoyle* 1297 (FHO), tree to 13 m., young leaves yellowish tomentose, browner on margin. Mporokoso Dist., a few km. S. of Chienge, nr. Lake Mweru, fl., frt., Nov. 1952, *White* 3623 (FHO), growing with *Acacia campylacantha* and *Piliostigma thonningii* in tall grassland on heavy clay soil fringing small stream, small tree 8 m. high with white fls.

ANGOLA. Malange Dist., Malange, fl., *Buchner* 564 (K). Lunda Dist., Chitato, nr. Luembe R., alt. 700 m., fl., June 1948, *Gossweiler* 14068 (K), in savannah; shrub-like tree 4 m. high with white strongly unpleasant-smelling fls.

Taxonomic history

T. torulosa was based on *Böhm* 142 a (fl.) from Gonda, Tanganyika; the type specimen has not been seen, but from the original description and the illustration by Engler and Diels in their monograph it is clearly conspecific with *T. mollis*. Engler and Diels include *Petherick* s.n. (the holotype of *T. mollis*) as a synonym of *T. torulosa*, although the former was described many years earlier and appears to be the legitimate name. They also cite *Schweinfurth* 1786! which is conspecific with *Petherick* s.n.

T. dewevrei was based on *Dewèvre* s.n.! (frt.) from the Belgian Congo; it only differs from *T. mollis* in the not so densely tomentose leaves.

T. spekei was based on *Speke & Grant* 643! (frt.) and *Dawe* 858! (fl., frt.), both from Uganda. It was stated by Rolfe to differ from *T. mollis* in the longer leaves; the type specimen, however, consists of leaves ranging from 15 to 32 cm. in length, which come well within the range of variation of *T. mollis*.

T. kerstingii was based on *Kersting* 476 (frt.) from Togo. *T. reticulata* was based on *Kersting* 476 a (frt.) also from Togo. The type specimens of these species have not been seen, but the descriptions agree with the West African material of *T. mollis*.

T. suberosa was based on *Fries* 264! (st.) and 264 a! (frt.), from Northern Rhodesia. *Fries* 264 is undoubtedly a coppice shoot and is variable in leaf-shape. *Fries* 264 a differs slightly in the much stouter branchlet, but this is no doubt due to the twig being several years old.

T. glandulosa was based on *Delevoy* 487! (frt.) and 301! (fl.), *Ritschard* 1506!, 1507! (frt.), 1506 bis!, 1507 bis! (frt.), all from the Belgian Congo. All the specimens come well within the range of variation of *T. mollis*.

Hutchinson and Dalziel (*Fl. West Trop. Afr.* **1**, 226 (1927)) maintain *T. kerstingii* and *T. reticulata* as separate species. Keay, in the second edition, brings the synonymy up to date by placing *T. torulosa*, *T. reticulata* and *T. kerstingii* as synonyms of *T. mollis*. Aubréville (*Fl. For. Soudano-Guinéenne*, p. 132 (1950)) maintains *T. dewevrei* as a separate species and includes *T. spekei*, *T. glandulosa* and *T. reticulata* as synonyms.

The Southern Rhodesian material (all fruiting) of *T. mollis* is atypical in the branchlets, which strongly resemble those of *T. stenostachya*, and in nervation and leaf-size, and has not been included in the citations. Further material is required, particularly correlated flowering and fruiting specimens. It is possible that here at the southern limits of its distribution it hybridizes with *T. stenostachya*. More information is required.

Distribution and ecology

T. mollis is very widely distributed; its western limit is in French Guinea according to Keay in *Fl. W. Trop. Afr.*, but no specimens from there have been examined by the present author; it occurs again in the Central Cameroons and parts of Ubangi Shari, and then shows an almost continuous distribution across the extreme northern parts of the Belgian Congo and the southern parts of the Equatoria Province of the Sudan Republic; farther south it extends through most of Uganda, western Kenya, western and central Tanganyika and Ruanda Urundi, through the Kwango, Tanganyika and Katanga districts of the Belgian Congo, and into the northern and western parts of Northern Rhodesia to as far south as Mazabuka District; it also occurs in the Lunda and Malange districts of Angola.

In the Cameroons (4) it occurs with *T. macroptera* in the savannah woodland on the Adamaoua Plateau. It forms one of the six principal trees in this type of savannah (3) (see under *T. macroptera*, p. 867).

In Ubangi Shari (3) it occurs in the dry forest of Leguminosae and *Anogeissus*, which extends over large areas of the Logone–Shari and Haut Kotto regions, as one of the species intermediate in height between the undergrowth and the forest trees, or replacing the forest trees.

In the Sudan Republic (28) it was found as one of the principal canopy trees in the shallow parts of the eluvial zone in 'ironstone woodland' at Wau and Aweil. At Wau it occurred as an occasional subcanopy tree in 'ironstone woodland', and at Aweil was rare as a canopy tree and as a member of the shrub layer as saplings or coppice in the *Combretum* zone (colluvial).

In many of its localities in Northern Belgian Congo, western and southern Uganda, western Kenya, Ruanda Urundi and north-western parts of Tanganyika, *T. mollis* occurs in the lower-montane derived savannah zone, containing remnants of rain-forest.

In the Karamoja District of Uganda (12) it occurs with *T. macroptera* and *T. glaucescens* on alluvial soils in the *Combretum*–other species open woodland, and with *T. glaucescens*, *Combretum binderanum* and *C. molle* (common on higher ground), in the woodland of the southern and western parts of the district as in the Labwar Hills and at Napak.

In the Tabora District of Tanganyika (15), near Kakoma, *T. mollis* occurs with *T. sericea* at edges of *mbugas* bordering mixed *miombo*-woodland; termite mounds with thicket-type of vegetation on the top are present, and *Afrormosia angolensis* is common between the mounds. Also in Tabora District (5), it occurs with *T. sericea* in the *Combretum–Afrormosia* community on the flood plains of the Igombe and Ugalla Rivers. *T. mollis* is common between termite mounds in this area.

In the Belgian Congo (11) *T. mollis* occurs with *Sterculia quinqueloba* and *Piliostigma reticulata* in the Haut Lomani region, which appears to occupy a zone of transition between the Guinéenne and the Soudano-Zambésienne floras. The *Terminalia–Bauhinia* savannah prefers the lighter soils in this region. *T. mollis* also occurs in the *miombo* region of Haut Katanga, and is very frequent in valleys, and on alluvial plains forms a *T. mollis–Acacia campylacantha* savannah with tall dense grass, as at Kasenga on the Luapula River. Its localities in western Belgian Congo (Kwango District) occur in a region containing a mixture of rain-forest and pseudosteppe.

In Northern Rhodesia it occurs mainly in the *miombo* regions, but characteristically on rejuvenated and alluvial soils (White, unpublished), and also in the seasonal swamp grasslands around Lake Bangweulu and Lusaka. Robbins (33) studied the Lusaka–Kafue River region and records *T. mollis* from the semi-swamp communities on alluvium, which occur between the true treeless swamp and the adjoining forest type. In this area the ground is sandy, but is more or less waterlogged in the rainy season owing to a pan or rock near the surface. It also occurs at the edge of dambos.

In Angola it is found in the region of *miombo* woodland, but little precise information on its ecology is available.

(20) **T. ivorensis*** A. Chev., *Vég. Ut. Afr. Trop. Franç.* **5**, 152 (1909); A. Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); Engl., *Pflanzenw. Afr.* **3** (**2**), 720 (1921); Aubrév., *Fl. For. Côte d'Ivoire*, **3**, 56 (1936); Kennedy, *For. Fl. Southern Nigeria*, p. 45 (1936); Burtt Davy & Hoyle, *Check-Lists For. Trees & Shrubs Brit. Emp.* **3** (Gold Coast), 36 (1937); Keay, *Fl. West Trop. Afr.*, ed. 2, **1** (**1**), 279 (1954).

Terminalia sp., Holland, *Kew Bull.* (Addit. Ser.), **9** (2), 308 (1909).

See Fig. 20. Tall, straight-boled tree, 15–30 m. high; bole bluntly buttressed and frequently fluted; branches in wide-spreading tiers; bark of bole light grey to dark brown, later almost black, longitudinally fissured, flaking in small scales; slash yellow; bark of branchlets smooth, with fine longitudinal fissures, greyish brown. *Lvs.* broadly oblanceolate to elliptic-obovate narrowed from above the middle to the base, apex abruptly and shortly acuminate, base obtuse to acute, 10·5 × 3–13·5 (–17·5) × 4·5 (–6·5) cm., glabrous except for minute hairs on petiole and midrib above and main nerves beneath, thinly coriaceous; *upper surface*: midrib strongly impressed, tertiary nerves conspicuously raised, and obscurely papillose; *lower surface*: midrib and secondary nerves very prominent, tertiary nerves scarcely raised, venation obscurely reticulate; petiole 2–2·5 cm. long. *Infl.* 6·5–9·5 cm. long, peduncle 2·5–3 cm. long, densely tomentose; *fl.*: lower receptacle densely tomentose, upper receptacle less so; calyx-lobes acuminate. *Frt.* narrowly oblong, apex obtuse, emarginate, base subtruncate or rounded and slightly decurrent, 5·8 × 1·7–10 × 2 cm., finely tomentose with very short reddish hairs, orange-brown; pedicel 0·7–1·1 cm. long.

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* In *T. ivorensis* the leaves are sparsely and minutely puberulous (appearing glabrous to the naked eye) with appressed hairs, and taper gradually to the base from very near the apex. The fruits are nearly always more than four times as long as broad. *T. glaucescens* east of the Cameroons is a different-looking plant with tomentose or densely pubescent leaves (spreading hairs), tapering from nearer the middle to both ends; its fruits are usually less than three times as long as broad. West African *T. glaucescens* is more or less intermediate; it shares habit and (usually) ecology with the eastern form, but is closer in leaf and fruit characters to *T. ivorensis*. (F.W.)

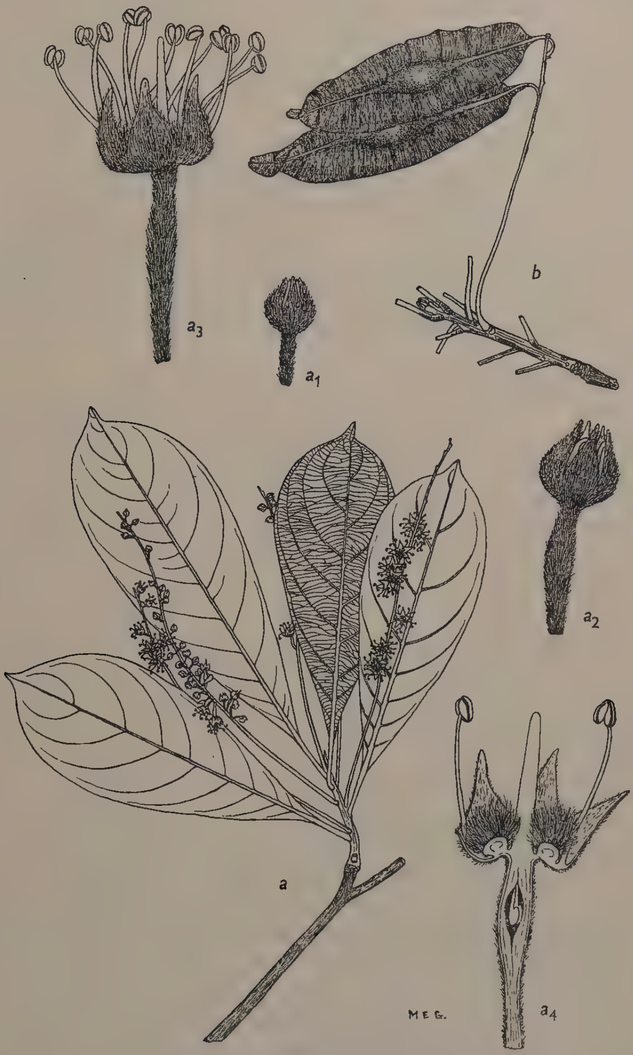

Fig. 20. *T. ivorensis* A. Chev. *a*, from *Deighton* 1142; a_1–a_4, from *Beveridge* 79; *b*, from *Andoh* 5816.

The leaves show no marked differences in size, and the shape remains fairly constant. The fruits vary somewhat in size, especially the width of the wings, but the general shape remains the same.

French Guinea. Cercle de Nzerekore, Nzerekore, frt., Oct. 1947, *Baldwin* 9716 (K), tree to 13 m. high.

Sierra Leone. Kenema Dist., Kambui Hills F. R., Waanje Valley nr. Kenema, Oct. 1953, Nov. 1953, Dec. 1953, Jan. 1954, Mar. 1954, all fruiting specimens from tree 'BS I' coll. by *Ranger Deen* (FHO). Moyamba Dist., Njala, fl., May 1928, *Deighton* 1142 (BM, K), common tree 17 m. high with horizontally spreading branches and white fls. Kambia Dist., Rokupr. frt., Feb. 1946, *Deighton* 4191 (K), tree commonly planted from Freetown northwards along Bullom coast to Scarcies R. for timber, especially in connexion with boat construction. Dist. unknown, no locality given, fl., *Lane-Poole* 276 (K), tree with firm deep red heartwood. Tonkolili Dist., Tonkoli F. R. nr. Sumbaria, Oct. 1953, Dec. 1953, Feb. 1954, all fruiting specimens; May 1954, flowering specimen; from tree 'T I', coll. by *Ranger Yongawo* (FHO), in high forest.

Liberia. Gbau, frt., Sept. 1947, *Baldwin* 9424 (K), tree to 25 m. high, 0·75 m. girth, wood soft. Dukwia R., fl., Apr. 1929, *Cooper* 370 (BM, FHO, K), tree 20 m. high, 0·3 m. girth, no buttresses, bark finely divided, cracked and plated, fls. fragrant.

Ivory Coast. Cercle de Man, Guiglo, fl., 1932, *Aubréville* 1226 (K). Cercle des Lagunes, Macouguie, frt., Jan. 1907, *Chevalier* 16153 (K, lectotype). Cercle de l'Agneby, Yapo, in forest, st., Oct. 1909, *Chevalier* 22329 (K). Banco, st., Sept. 1931, *Service Forestier* 475 (FHO).

Ghana. Wasaw Aowin Dist., Hemang, frt., Nov. 1953, *Andoh* 5816 (FHO), tree 15 m. high, 1 m. girth. Birim Dist., Mpraeso, alt. 580 m., fl., Apr. 1934, *Beveridge* 79 (FHO, K), in deciduous forest, tree 26 m. high, shallow crown with wide-spreading flat branches, bark dark, wood yellow, lustrous, splits well. Cape Coast Dist., Akotoase, frt., Sept. 1913, *Chipp* 569 (K), common tree, bark prominently ribbed, dark, wood yellow. Wasaw–Aowin Dist., Yakasi, 6 km. W. of Enchi, fl., July 1939, *Foggie* 205 (FHO), tree 25–30 m. high, specimen collected from crown of wind-blown tree. Dist. unknown, nr. Dunkwa, st., Feb. 1927, *Vigne* 260 (K), tall tree, young trees with smooth, pale bark, older trees with rough, dark bark, wood yellow.

Nigeria. Benin Div., Okomu F. R., frt., Nov. 1936, *Hide* 31/37 (FHO). No locality given, frt., *Kennedy* 1579 (FHO). Ondo Div., Ofaro-Oluwa, frt., July 1909, *Kitson* s.n. (BM), small tree. Ilaro Div., Ilaro, frt., Sept. 1928, *MacGregor* 342 (FHO), medium-sized tree in deciduous forest, bark light grey, no buttressing, older trees with dark bark and wide-spreading crowns.

British Cameroons. Cameroons Div., Okoyong, Mamfe on Cross R., alt. 200 m., frt., July 1931, *Johnstone* 149/31 (FHO), tree in mixed deciduous forest.

Local uses. *T. ivorensis* is used locally in West Africa for various household purposes—as beams, or merely as a framework for mud houses, shingles, rice-mortars, and for boat construction (canoes). The yellowish red dye extracted from the bark is used for dyeing cotton cloth and vegetable fibres used for basket work. Also used locally for furniture, carpentry and general indoor constructional work.

European uses. The timber market names are 'Idigbo' and 'Framiré'.

The wood is yellow, it saws, planes, and splits easily, and takes a good polish. The timber floats and is liable to attack by termites.

Rendle (*Emp. For. Rev.* **33**, 319 (1954)) states that secondary, heavy timbers like *T. ivorensis* are not likely to be imported to Europe in quantity unless shipping companies adopt a system of freight charges based on measurement rather than on weight.

Distribution and ecology

T. ivorensis does not appear to be so widely distributed as *T. superba*; it occurs at various localities throughout the rain-forest zone from French Guinea to the British Cameroons, but, unlike *T. superba*, it has not been recorded from farther east than the latter territory.

It commonly occurs with *T. superba* in 'deciduous' rain-forest, and shows some of the latter's characteristics in that it is also a strong light demander, a good colonizer of abandoned farmland, and also occurs as an emergent species in the upper storey.

In the Ivory Coast (2) it is abundant in secondary and primary forest in the deciduous forest zone, especially in the transition to the rain-forest zone. It occurs in the latter in the parts deforested by cultivation. It is dominant in some regions—Agboville, Tiassalé, Kouta and Gagnoa.

In Ghana (35) it occurs with *T. superba* in the *Celtis–Triplochiton* association occupying a region south of the Kwahu–Mampong scarps. Chipp (6) records it from a number of vegetation types in which *T. superba* also occurs, and in addition it occurs in the *Tarrietia–Anopyxis* associes in areas subjected to inundation for short periods, occupying the low-lying country in the south-west.

In Nigeria, according to MacGregor (24), it is confined to the best types of deciduous forest and rain-forest, and its 'minimum habitat' is probably in the mixed deciduous forest of Ondo. It is absent from the Olokemeji forests but appears again as an invasive species in the Mamu forests.

It is an intense light demander from the seedling stage onwards; the seedlings require a rainfall of 1375 mm. (55 in.) or more, and full light. The young plants grow at a very rapid rate and show an annual increase of about 3 cm. in diameter.

(21) **T. glaucescens** Planch. ex Benth. in Hook., *Niger Fl.* p. 336 (1849); Laws., *Fl. Trop. Afr.* **2**, 416 (1871); Engl. & Diels, *Monogr.* **4**, 13, t. 4 B (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 721 (1921); Kennedy, *For. Fl. Southern Nigeria*, p. 45 (1936); Burtt Davy & Hoyle, *Check-Lists For. Trees & Shrubs Brit. Emp.* **3** (Gold Coast), 35 (1937); Aubrév., *Fl. For. Soudano-Guinéenne*, p. 132 (1950); Keay, *Fl. West Trop. Afr.* ed. 2, **1** (**1**), 279 (1954).

T. schimperana Hochst. ex Delile in Ferret & Galin., *Voy. Abyss.* **3**, 133 (1848), nomen pro syn. sub. *T. avicennioides*; Hochst. ex Engl. & Diels, *op. cit.* 14, descr. t. 4 D (1900); Engl., *op. cit.* 722 (1921); Pichi-Sermolli, *Miss. Stud. Lago Tana*, **1**, 101 (1951).

T. baumannii Engl. & Diels, *op. cit.* 14, t. 6 A (1900); A. Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); Engl., *op. cit.* 721 (1921).

T. passargei Engl. ex Engl. & Diels, *op. cit.* 16, t. 7 A (1900); Engl., *Jahrb.*, **39**, 512 (1907); A Chev., *op. cit.* 256; Engl., *op. cit.* 721 (1921).

T. togoensis Engl. & Diels, *op. cit.* 13, t. 5 B (1900); Holland, *Kew Bull.* (Addit. Ser.) **9** (**2**), 307 (1909); A. Chev., *Études Fl. Afr. Centr. Franç.* **1**, 119 (1913); A. Chev., *op. cit.* 256 (1920); Engl., *op. cit.* 721 (1921).

T. velutina Rolfe, *J. Linn. Soc.* (*Bot.*), **37**, 517 (1906); Engl., *op. cit.* 721 (1921); Eggeling, *Indigenous Trees Uganda Prot.*, ed. 1, 48 (1940), Eggeling & Dale, *op. cit.* ed. 2, 93 (1951).

T. longipes Engl., *op. cit.* 513 (1907); Engl., *op. cit.* 721 (1921).

T. excelsior A. Chev., *Sudania*, **1**, 121, no. 7548 (1911), nom. nud.; A. Chev., *op. cit.* 119 (1913), nom. nud., synon. nov.

T. flava Engl., *op. cit.* 722 (1921), synon. nov.

See Fig. 21. Small tree, 7–13 m. high, with open, rounded, spreading crown; bark of bole light or dark grey to black, rough, deeply and longitudinally furrowed; slash red, fibrous, OB irregular, brown, IB reddish brown to yellow; sapwood yellow; bark of branchlets dark reddish brown or light brown, with fine longitudinal fissures. *Lvs.* broadly oblanceolate-elliptic, elliptic or broadly oblong-lanceolate, apex obtuse to acute or shortly acuminate, base acute to rounded, 15×5–$22{\cdot}5\ (-27{\cdot}2) \times 7{\cdot}8\ (-8{\cdot}2)$ cm., young leaves densely tomentose, older leaves glabrous above except for midrib, densely sericeous-tomentose beneath on main nerves and sparsely pubescent on tertiary nerves, slightly undulate, chartaceous, dark green above, light green and rather glaucous beneath; *upper surface*: midrib and secondary nerves flattened or slightly impressed, tertiary nerves raised and obscurely papillose; *lower surface*: midrib and secondary nerves very prominent, tertiary nerves and venation conspicuous but not raised; petiole 2·5–4 cm. long. *Infl.* 7–10·9 cm. long, peduncle 1·5–2 cm. long, densely tomentose, *fl.*:

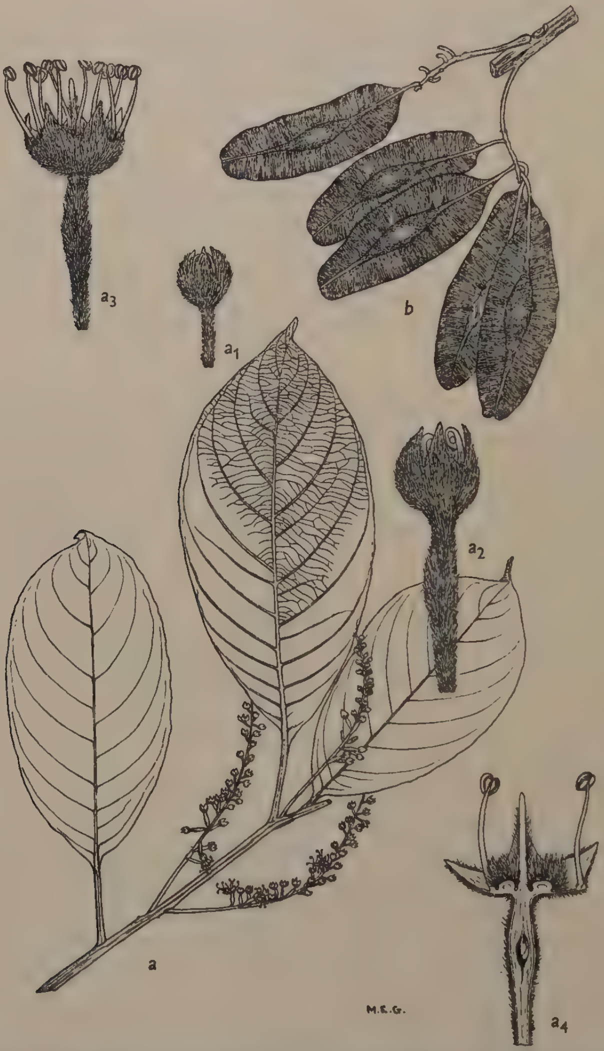

Fig. 21. *T. glaucescens* Planch. ex Benth. *a*, from *Kitson* 1104; a_1–a_4, from *Vigne* 1917; *b*, from *Vigne* 3314.

lower receptacle densely sericeous-tomentose, upper receptacle less so; calyx-lobes acute. *Frt.* narrowly oblong to oblong-elliptic, apex obtuse to truncate, usually emarginate, base obtuse to rounded, 5·5 × 1·5–7·5 × 2·2 cm., finely tomentose, brown; pedicel 0·5–0·7 cm. long.

The leaves are very variable in size, but the general shape remains fairly constant, that is, more or less elliptic. The amount of indumentum on the leaves varies considerably, see under 'taxonomic history'. The fruits show no marked variation in shape and no appreciable difference in size, except occasionally in the width of the wings.

French Guinea. Kouria, frt., Aug. 1905, *Chevalier* 14695 (K).

Sierra Leone. Koinadugu Dist., Mussaia, frt., Feb. 1946, *Deighton* 4223 (K), rather gnarled tree 7–8 m. high. Id., Kabala, fl., July 1948, *Deighton* 4817 (K), in orchard bush, tree 8 m. high with greenish white, unpleasant-smelling fls. Id., Musaia, fls., July 1948, *Deighton* 4821 (K). Id., Gberia Fotumba, about 19 km. E. of Falaba, frt., Oct. 1951, *Small* 343 (K), common with *Uapaca*, *Daniellia*, tree 10–13 m. high, leaves pubescent, frt. tomentose. Tonkolili Dist., Tonkoli F. R. nr. Sumbaria, Nov. 1953, Jan. 1954, Mar. 1954, all fruiting specimens from tree 'TF I' coll. by *Ranger Yongawo* (FHO), tree in savannah woodland.

Ivory Coast. Cercle de Bondoukou, Bondoukou, frt., *Aubréville* 1600 (K). N. of middle Nzi Valley, between Felekro and Tiebissou, fl., July 1909, *Chevalier* 22194 (K). Cercle du Baoule, N. of middle Nzi Valley nr. Languira, frt., July 1909, *Chevalier* 22204 (K), in savannah.

Ghana. Volta R. Dist., Kpeve, fl., May 1926, *Gent* 107 (FHO), common tree of savannah, last of savannah trees to come into leaf. Birim Dist., Adumasia to Pabarabo Hill, Afram Plains, fl., May 1928, *Kitson* 1104 (K), fair-sized tree. Dagomba Dist., Yendi, alt. 240 m., fl., Apr. 1929, *Vigne* 1692 (FHO), in savannah forest, tree 6 m. high. Mampong Dist., Mampong, fl., *Vigne* 1917 (EA, FHO, K), tree in savannah forest and extending into transition forest. Gonja Dist., Yeji, alt. 140 m., frt., Aug. 1934, *Vigne* 3314 (BM, FHO), in fringing forest near Volta R., tree 8 m. high, 0·6 m. girth.

Togo. Ho Dist., Hohoe, alt. 160 m., fl., May 1933, *Beveridge* 49 (FHO), in savannah woodland, spreading tree 6 m. high, bark deeply furrowed, slash red, fls. pale green. Nr Lome, 1900–1902, frt., *Warnecke* 442 (BM, EA, K).

Dahomey. Cercle de l'Atacora, Mt. Atacora, Somba country, Toukountounna to Tangueta, alt. 300–600 m., fl., June 1910, *Chevalier* 24089 (K).

Nigeria. Aboh Div., Aboh on Niger R., frt., *Barter* 330 (K), small tree. Zaria Div., Gurara R., nr. Gornapara, frt., July 1906, *Elliot* 186 (K). Ibadan Div., Awba Hills F. R. frt., Oct. 1943, *A. P. D. Jones* FHI 7301 (K), open savannah woodland to secondary high forest transition, tree 12 m. high, 0·6 m. girth, gnarled and twisted, bark deeply fissured, dark grey, OB 2 cm. thick, irregular, brown, IB reddish brown to ochrous yellow, fibrous, sapwood yellow. Ikom Div., Ikom, fl., *Rosevear* 48/29 (FHO, K), in savannah. Kabba Prov., Lokoja, on the Quorria at Attah, frt., *Vogel* 178 (K, holotype), medium-sized tree.

Ubangi Shari. Dar Kuti Occidental, Ndele, frt., Feb. 1903, *Chevalier* 7548 (P), common on the rugged slopes, tree 8–20 m. high, trunk usually straight in older trees, 10 m. to first branch. Id., frt., Feb. 1903, *Chevalier* 7660 (K). Moyen Logone, Buar, alt. about 1000 m., fl., May 1914, *Mildbraed* 9502, 9508 (K).

British Cameroons. Bamenda Div., Bamenda, Fang, alt. 1000 m., fl., Apr. 1931, *Maitland* 1404 (K), frequent tree throughout Bamenda up to 1700 m. alt.

French Cameroons. Sansane, alt. about 750 m., fl., Apr. 1914, *Mildbraed* 8951 (K). Mbussa, alt. 800–900 m., fl., Apr. 1914, *Mildbraed* 9095 (K). Kuare, alt. 950 m., fl., May 1914, *Mildbraed* 9231 (K). Yaunde, fl., 1897, *Zenker* 1421 (K), in woodland.

Belgian Congo. Uele Dist., between Uele and Gwane, fl., May 1931, *Lebrun* 2883 (BR), in savannah woodland, tree 6–8 m. high, branching from base, light crown, bark dark reddish grey, fls. greenish. Id., between Amadi and Poko, fl., June 1931, *Lebrun* 3069 (BR), large tree about 8 m. high with yellow fls. Id., between Amadi and Doruma, fls., June 1931, *Lebrun* 3136, (BR), in savannah woodland, tree 7 m. high, open umbrella-shaped crown, bark deeply fissured, dark grey, fls. greenish white. Kibali Ituri Dist., Nabundunda Village, between Maika R. and Niangara–Wamba Rd., frt., July 1937, *Louis* 4438 (K). Uele Dist., Garamba National Park, Wilibadi, alt. 800 m., fl., July 1948, *Robyns* 3100 (BR), in dry savannah woodland, tree 10–12 m. high with open crown and greenish fls.

ETHIOPIA. No locality or date given, but probably collected in Shire country, frt., *Quartin-Dillon & Petit* 30 (K). Djelajeranne, fl., Aug. 1841, *Schimper* 1638 (K, syntype of *T. schimperana*).

SUDAN REPUBLIC. Equatoria Prov., nr. Sakor Resthouse, Yambio, fl., May 1939, *Andrews* 1522 (K), occasional medium-sized tree, bark rough, black, fls. light yellow. Blue Nile Prov., Khôr Offat, frt., Feb. 1924, *Aylmer* 15 (SGH), on rocky ground. Id., Gallabat, fl., June 1931, *Cooke* 46 (SGH), medium-sized tree up to 13 m. high, trunk fairly smooth, mid-grey, fls. greyish white. Equatoria Prov., 2 km. S.W. of Mapare Village, 3–5 km. along Aweil–Nyambell Rd., frt., Feb. 1939, *Hoyle* 614 (FHO), in deciduous woodland on ironstone, small slender tree with ascending spreading crown of slender branches, bark fissured, lightish grey, Id., Imatong Mts., Katire along Kineti R., alt. 1200 m., frt., Dec. 1935, *Thomas* 1564 (BM), abundant, spreading tree 10 m. high, 1 m. girth, bark deeply ribbed.

UGANDA. Karamoja Dist., Labwor Hills, fl., Feb. 1937, *Brasnett* 180 (FHO), small tree, bark rough, corrugated. Busoga Dist., precise locality not given, alt. 1300 m., fl., frt., July 1905, *Brown* 260 (K, syntype of *T. velutina*). Bunyoro Dist., Nkusi R., frt., 1905, *Dawe* 697 (K, syntype of *T. velutina*). Mengo Dist., Busana, Bugerere, alt. 1300 m., fl., *Eggeling* 437 (EA, FHO). Acholi Dist., Gulu, frt., *Eggeling* 765 (EA), tree to 13 m. high.

Taxonomic history

Delile (in Ferret and Galinier's *Voy. Abyss.* 3, 133 (1848)) first published Hochstetter's name—*T. schimperana*—as a possible synonym of *T. avicennioides*. Engler and Diels were the first authors to regard it as a good species and they described it in their monograph; they cite as type specimens *Schimper* 1638! (fl.) and *Schimper* 1679. The leaves of *Schimper* 1638 are densely hairy, but this is a characteristic feature of *T. glaucescens* at higher altitudes, and scarcely justifies specific status.

T. baumannii was based on *Baumann* 262 (fl.) from Togo. *T. passargei* was based on *Passarge* 110 (fl.) from the Benue area of Nigeria. *T. togoensis* was based on *Büttner* 155 (frt.) from Togo. These three species were described at the same time, and show only slight variation in the size of the leaves. None of the type material has been seen, but from the descriptions and illustrations in Engler and Diels's monograph they are all conspecific with *T. glaucescens*.

T. velutina was based on *Brown* 260! (fl., frt.) and *Dawe* 697! (frt.) from Uganda. It differs from *T. glaucescens* in the densely hairy leaves, resembling *Schimper* 1638, but it certainly comes within the range of variation of *T. glaucescens*.

T. longipes was based on *Kersting* 639 (fl.) from Togo. The type has not been seen, but judging from the description it is conspecific with *T. glaucescens*.

T. excelsior based on *Chevalier* 7548! (frt.) is a nomen nudum; it is listed in Chevalier's *Sudania*, 1, 121 (1911). The specimen consists of a few old leaves and several detached fruits; it comes within the range of variation of *T. glaucescens*.

Engler does not mention the specimens on which *T. flava* was based, and does not give a full description. Several specimens collected near the type locality in the Cameroons and sent from Berlin to Kew under this name show that it is close to *T. schimperana* and *T. velutina* in having densely hairy leaves and is clearly conspecific with *T. glaucescens*.

Hutchinson and Dalziel (*Fl. West Trop. Afr.* 1, 226 (1927)) include *T. passargei*, *T. togoensis*, *T. longipes* and *T. baumannii* as synonyms of *T. glaucescens*, a view which is maintained by Keay in the second edition of the Flora.

The species mentioned under the name of *T. avicennioides* by A. Rich. (*Tent. Fl. Abyss.* 1, 264 (1848)) and by Andrews (*Flowering Plants of the Anglo-Egyptian Sudan*, 1, 210 (1950)) is probably *T. glaucescens*, since the former species is otherwise not known to occur farther east than Ubangi Shari; unfortunately no specimens are cited in the second work so that these records cannot be checked.

The record for *T. avicennioides* in Burtt Davy *et al.*, *Check-Lists For. Trees & Shrubs Brit. Emp.* 1 (Uganda Prot.), 37 (1935) is an error for *T. glaucescens*; the following specimens which are cited have been seen—*Eggeling* 1162, *Forest Department* 712 and 1334. Eggeling (*Indigenous Trees of Uganda*, p. 48 (1940)) points out this error.

Distribution and ecology

T. glaucescens is a common tree in the Southern and Northern Guinea Zones of West Africa, where it extends from Sierra Leone to the southern Cameroons and north-east to Ubangi Shari; it also occurs in the Uele and Kibali Ituri districts of the Belgian Congo, Equatoria and Blue Nile Provinces of the Sudan Republic, and penetrates as far south as Busoga District of Uganda; its eastern limit is in the Shiré country of northern Ethiopia.

It is one of the first components of savannah woodland to be encountered after the northern edge of the rain-forest zone is left behind, and is one of the first pioneer species in the savannah which succeeds destroyed rain-forest (4).

It is found in abundance (4) in the Kissidougou District of French Guinea; and in the central Ivory Coast it is also abundant from Ferkéssédougou to the northern edge of the closed rain-forest of the south; towards the north it appears to stop at the border of the Sudan Zone proper, following a line from Kankan to Ferkéssédougou. It is frequently found in gallery forest.

In Ghana (6) it is one of the first savannah woodland species to be encountered in the fringing forest north of Ejura, and is also present in the *Uapaca heudelottii–Hymenocardia acida* associes found in this area. The *T. glaucescens–Vitex doniana* associes is typical in burnt-over, dry, grassy areas, such as around Kobresu in western Ashanti, and Kumawo in central-eastern Ashanti.

In the Zamfara Forest Reserve (20) of the Sokoto Province of Nigeria, *Acacia campylacantha* forms a more or less pure open savannah woodland on alluvial soils, but in the more disturbed areas it becomes mixed with *A. sieberana* and *Piliostigma thonningii* and very occasionally with *T. glaucescens*; here the latter is in the Sudan Zone. It is a typical species in the Southern Guinea zone in Nigeria (19) on low-lying ground, for example flood plains with heavy clay soils, tall grass and only a few widely spaced trees of specialized species. It also occurs with *Borassus* on the flood plains of wide river valleys with tall grass, and, often together with *Anogeissus schimperi*, completely replaces *Isoberlinia doka* woodland on certain areas adjoining streams of flood plains. In the Northern Guinea zone this moist *Anogeissus–T. glaucescens* woodland (21), with very tall grass and *Ensete* and *Nauclea* in the undergrowth, usually occurs between the *I. doka* woodland and the valley grasslands. In the *Hyparrhenia cyanescens* valley grassland, *T. glaucescens* and *Piliostigma thonningii* form shrubby clumps, which are overtopped by the grass in the rainy season. In the Northern Guinea zone (20) *T. glaucescens*, *Vitex doniana* and *Khaya senegalensis* occur as widely spaced emergents in fringing forest, and (21) where fire pierces the latter it merges into a belt of transition to the savannah woodland; the first two species are two of the commonest species found in the transition zone.

It is abundant in open savannah woodland on the Adamaoua Plateau of the Cameroons (4), especially towards the south until the closed forest is reached. It is common (3) south-west of this plateau, between Ngaoundéré and Tibati, occurring in patches of low dry forest.

In the Ubangi Shari (Aubréville, 3), it is abundant in the dry *Anogeissus* forest of the Yalinga to Bakouma region. Near Djema it is also abundant in another of Aubréville's forest types—*Anogeissus–Albizia* dry forest transitional to rain-forest, where this latter occurs on alluvial soils; when this forest type is degraded by fire (near Obo, for instance) it is also abundant. In the dry forest of Leguminosae and *Anogeissus* in the Logone-Chari area, *T. glaucescens* is often found gregarious and behaves as a pioneer species on abandoned farmland. It is frequent in the *Burkea–Lophira* savannah woodland in the Haut Sangha region. The Bangassou to Bambari area, which is occupied by a dry savannah type in which *Daniellia oliveri* is a characteristic tree, is a region where closed forest is regressing and *T. glaucescens* is one of the colonizing species.

In the Sudan Republic (28) it occurred as part of the main upper canopy (but is rather rare) in the eluvial zone of 'ironstone woodland' at Aweil.

T. glaucescens and *Combretum binderanum* are two of the commonest species found towards the top of the escarpment in the Büso area of the Budongo Forest of Uganda (13); here the soil is poorer and the climate drier than elsewhere in the forest reserve. *T. glaucescens* often forms a fairly dense stand. It is also very common with *Vitex doniana* and *Combretum molle* on Busingiro Hill and Little Kasenene Hill (the only grass covered hill in the Forest). In the northern and north-eastern parts of the Forest, where the soil is richer and the climate wetter, it has been found to play an important part in the succession from derived savannah to rain-forest. Eggeling was able to make use of its behaviour here, in elucidating the history of the forest. It also occurs in the Karamoja District (12) and is common with *T. macroptera* and *T. mollis* on alluvial soils in the *Combretum*–other species open woodland. In the woodlands of the southern and western parts of the Karamoja District (36) as at the base of Labwor Hills and at Napak it occurs with *T. mollis, Combretum binderanum* and *C. molle* (common on higher ground).

It is common around Lake Tana in Ethiopia (30) in vegetation bordering the montane types.

(22) **T. avicennioides** Guill. & Perr., *Fl. Senegamb. Tent.* **1**, 276, t. 64 (1832); Laws., *Fl. Trop. Afr.* **2**, 416 (1871); Engl. & Diels, *Monogr.* **4**, 14, t. 4 C (1900); Engl., *Jahrb.* **39**, 512 (1907); A. Chev., *Études Fl. Afr. Centr. Franç.* **1**, 119 (1913); A. Chev., *Expl. Bot. Afr. Occ. Franç.* **1**, 256 (1920); Engl., *Pflanzenw. Afr.* **3** (2), 721 (1921); *Aubrév., Fl. For. Soudano-Guinéenne*, 133 (1950); Keay, *Fl. West. Trop. Afr.*, ed. 2, **1** (1), 279 (1954).

T. lecardii Engl. & Diels, *op. cit.* 15, t. 6 B (1900); Engl., *op. cit.* 512 (1907); A. Chev., *op. cit.* 119 (1913); A. Chev., *op. cit.* 256 (1920); Engl., *op. cit.* 722 (1921).

T. dictyoneura Diels in Engl., *op. cit.* 512 (1907); Engl., *op. cit.* 722 (1921).

See Fig. 22. Shrub, 2–4 m. high, or small tree, 8–12 m. high, crown wide-spreading, bark of bole dark grey, rough, deeply fissured longitudinally and transversely; slash moist, scented, fairly hard, OB dirty brown, IB yellow; sapwood yellow; bark of branchlets densely tomentose, becoming grey and finely and longitudinally fissured with age. *Lvs.* oblong-lanceolate to narrowly oblong-elliptic, apex obtuse to rounded, base obtuse to acute, 11 × 3·5–19·5 × 6 cm., young leaves densely tomentose, older leaves glabrous except for midrib above, usually remaining tomentose beneath but at time of fruiting occasionally almost glabrous, slightly undulate, subcoriaceous, matt above; *upper surface*: midrib flattened, secondary nerves slightly impressed, tertiary nerves and venation raised; *lower surface*: midrib and secondary nerves prominent, tertiary nerves and venation subprominent; petiole 1–2·5 cm. long. *Infl.* 6–11 cm. long, peduncle 0·7–1·5 cm. long, densely tomentose; *fl.*: upper and lower receptacle densely tomentose; calyx-lobes subacute; style pilose. *Frt.* broadly oblong-lanceolate to elliptic, apex obtuse, style frequently persistent, base obtuse, 5·5 × 2·5–7·5 × 2·7 cm., densely velutinous-tomentose; pedicel 0·5–0·8 cm. long.

SENEGAL. No locality or collector's name given, fl., 1837 (K, OXF).

GAMBIA. N. bank of Gambia R., fl., July 1893, *Kanne* 12 (K).

PORTUGUESE GUINEA. Gabú, Canjadúdi, frt., Apr. 1949, *Espírito Santo* 2512 (K), tree 2 m. high, in savannah.

SIERRA LEONE. No locality or date given, fl., *Hutton* s.n. (K).

IVORY COAST. No locality given, frt., Mar. 1935, *Service Forestier* 1975 (K).

Ghana. Mamprusi Dist., Navrongo, fl., May 1948, *Andoh* 5185 (FHO), common in savannah forest, shrub to small tree with yellowish white fls. Wa Dist., Sekai to Boguboi, frt., Apr. 1927, *Kitson* 819 (K). Gonja Dist., Ypala to Kulmasa, fl., frt., Feb. 1927, *Kitson* 864 (K). Dagomba Dist., Tamale Mts., fl., Apr. 1928, *Lloyd Williams* 124 (K), in dry savannah, fairly common, small, thin shrub, with greyish leaves. Mamprusi Dist., Bawku, fl., Apr. 1935, *Vigne* 3763 (K), common savannah tree 8 m. high, 0·6 m. girth, spreading crown.

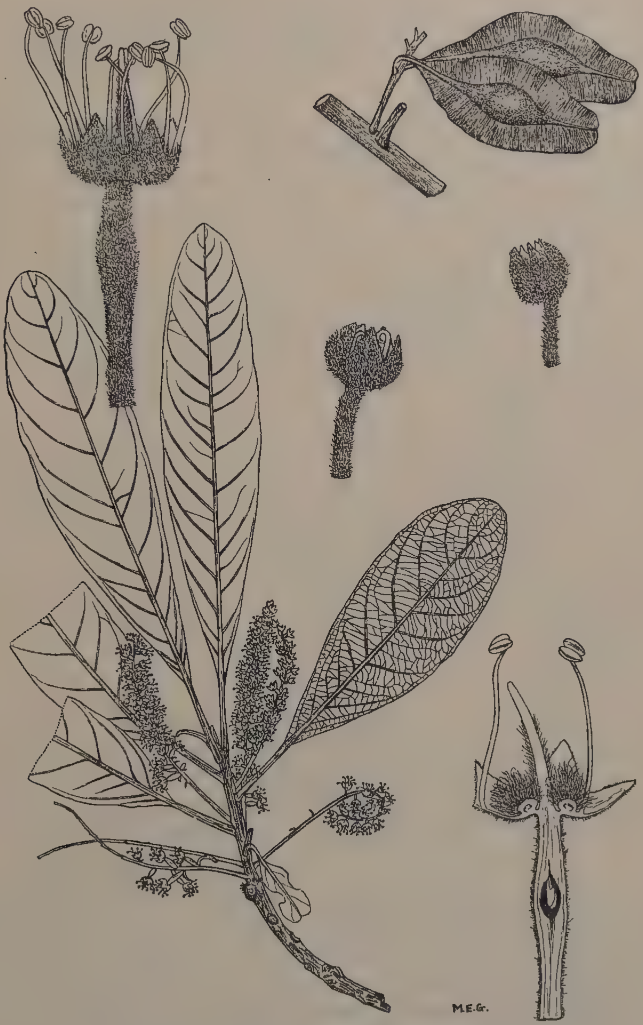

Fig. 22. *T. avicennioides* Guill. & Perr. Flowering specimen from *Keay* FHI 15886. Fruiting specimen from *Ogua* FHI 7952.

Togo. Sokode, frt., Mar. 1905, *Kersting* 32 (K, isotype of *T. dictyoneura*).

Dahomey. Nr. Agouagou, fl., May 1910, *Chevalier* 23513 (K). Cercle de Savalou, between Cabolé and Bassila, frt., May 1910, *Chevalier* 23798 (K).

Nigeria. Bida Div., Nupe country, fl., *Barter* 1120 (K, syntype of *T. lecardii*), common tree among scrub of the plains. Sokoto Div., Zamfara F. R., 13 km. from Zurmi on W. side of Farfara R., fl., Apr. 1946, *Keay* FHI 15886 (FHO, K), tree 6 m. high, 0·8 m. girth, erect bole for 1–2 m. below branches, bole rough, fissured, slash moist, scented, hard, OB dirty brown, IB yellow, sapwood dirty yellow, fls. yellow. Oyo Div., Old Oyo F. R. on left side of Ile stream about 2 km. E. of Tessi R., fl., Feb. 1946, *Keay* FHI 16278 (BM, FHO, K), in more or less high-level open savannah woodland with *Burkea*, *Bauhinia* and *Combretum*, tree 5 m. high, bark dark grey, deeply fissured, burnt, young leaves brownish pink above, pale green beneath. Bauchi Div., Bauchi Plateau, fl., frt., *Lely* 856 (K). Anchau Div., Rarfi-gaude, frt., May 1944, *Ogua* FHI 7592 (FHO), in open savannah woodland, small tree 3–4 m. high, 0·18 m. girth, bark rough, with ashy-grey scales, slash yellow, darkening rapidly, sapwood light in colour.

UBANGI SHARI. Dar Kuti Occidental, Mamoun country, Ndele area Dar-Goulla, between Ni and Gosso, frt., Feb. 1903, *Chevalier* 7764 (K), in woodland.

Taxonomic history

T. avicennioides was based on specimens collected by Perrottet in 1829 at Albreda in Gambia, although this material has not been seen the species known under this name agrees with the illustrations and description by Guillemin & Perrottet (*Fl. Senegamb. Tent.* **1**, 267, t. 64 (1832)).

T. lecardii was based on *Lécard* 229 (frt.) from Senegal, and *Barter* 1120! (fl.) and *Rowland* s.n.! (fl., frt.) from Nigeria; Engler and Diels do not indicate which specimen is the holotype. *Barter* 1120 and *Rowland* s.n. are again cited by Engler and Diels, this time under *T. avicennioides*, which suggests that the authors' views on these two species were somewhat confused! Both specimens are definitely conspecific with the other material of *T. avicennioides*.

T. dictyoneura was based on *Kersting* 32! (frt.) from Togo, and differs only slightly from the type material of *T. avicennioides*, as figured by Guillemin and Perrottet (*op. cit.*). The measurements of the leaves show no appreciable difference in size; in *T. dictyoneura* 10–18 × 4·6–6 cm., petiole 3–4 cm. long; in *T. avicennioides* 10·5–13 × 4–5 cm., petiole 2·5 cm. long; the former comes well within the range of variation of *T. avicennioides*.

Both Hutchinson and Dalziel (*Fl. West. Trop. Afr.* **1**, 226 (1927)) and Keay (ed. 2, *op. cit.*) include *T. lecardii* and *T. dictyoneura* as synonyms of *T. avicennioides*.

Distribution and ecology

T. avicennioides is widespread throughout the Sudan Zone from Senegal to Tchad Colony. At its northern limit it penetrates into the Sahel Zone on the alluvial soils of the colony west of Lake Tchad (10), where, with *Prosopis africana*, it forms an association on the low-lying, sandy plain south of Zinder. This community is of the highest type found in the territory. *T. avicennioides* is often locally dominant, especially on old cultivated ground. It forms a *Combretum–Terminalia* association on the laterite plateaux of the Niamey–Filingué–Tahoua–Madaoua region. Aubréville (4) records it as particularly abundant in the Gourma area between Fada N'Gourma and Tessaoua, but here it is very rare, and appears to be at the extreme limit of its distribution. Its eastern limit is about 100 km. east of Zinder. Its southern limit is at the northern edge of the Southern Guinea zone, and in the Ivory Coast (4) it reaches the northern edge of the closed forest, but does not appear to extend to the Banfora Cliffs farther south.

In the Sudan zone in central Nigeria (19) *T. avicennioides*, *Combretum glutinosum* and *Strychnos spinosa* are the commonest of the smaller trees, and, on the sandy soils of the east, the two former species with *Acacia senegal* and *Commiphora* spp. are abundant in the lower story of savannah woodland vegetation. In the Northern Guinea zone in Nigeria (19) pure communities of *T. avicennioides* and *Piliostigma thonningii* may replace *Isoberlinia doka* woodland on abandoned farmland. *T. avicennioides–Butyrospermum parkii* farmed savannah (21) is a secondary community which appears to replace *Isoberlinia doka* woodland when the latter is heavily farmed and burnt; *T. avicennioides* forms a low and often dense growth.

In the Ubangi Shari (3) it is common in the dry *Anogeissus* forest between Yalinga and Bakouma on the alluvial plains of the Chari to just south of Fort Lamy. This type appears to mark the transition to the xerophilous Sahel-Sudan zone.

In the northern parts of the Cameroons (3) it occurs in the spiny savannah or steppe savannah in which *Acacia* spp. predominate, occupying the region Mora-Dikoa-Fort Lamy-Maroua (in the Sahel zone).

(23) **T. albida** Scott Elliot, *J. Linn. Soc.* (*Bot.*), **30**, 79 (1894); Aubrév., *Fl. For. Soudano-Guinéenne*, p. 133 (1950); Keay, *Fl. West Trop. Afr.* ed. 2, **1** (**1**), 279 (1954).

T. argyrophylla Engl. & Diels, *Monogr.* **4**, 15, *t.* 6 C (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 722 (1921); non *T. argyrophylla* King & Prain (1898).

See Fig. 23. Shrub or small tree, 3–12 m. high, with well-developed crown; bark of branchlets densely sericeous-tomentose, becoming finely and longitudinally fissured,

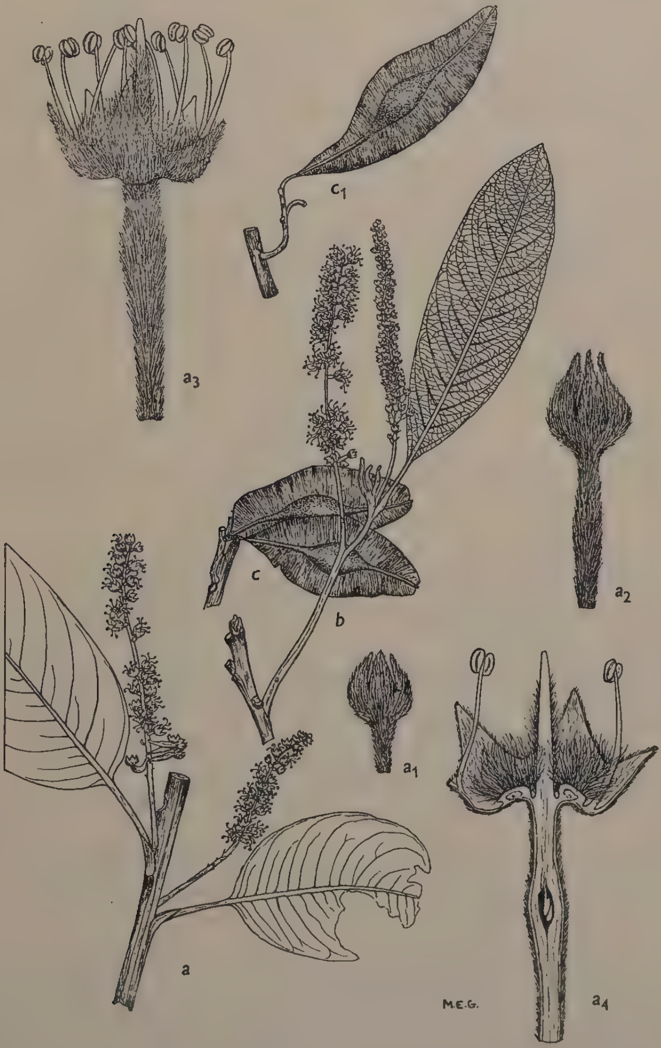

Fig. 23. *T. albida* Scott Elliot. *a*, a_1–a_4, from *Adames* 172; *b*, from *Fox* 110; *c*, from *Fox* 83; c_1, from *Small* 139.

grey to dark brown with age. *Lvs.* oblong-lanceolate to narrowly elliptic, apex acute or shortly acuminate, base obtuse to rounded, 11 × 2·8–16·5 × 5·5 cm., young leaves densely sericeous-tomentose, older leaves glabrous and shining above, usually remaining sericeous-tomentose beneath, subcoriaceous; *upper surface*: shining, midrib and secondary nerves slightly impressed, tertiary nerves and venation slightly raised; *lower surface*: midrib and secondary nerves prominent, tertiary nerves and venation subprominent; petiole 1–3 cm. long. *Infl.* 6–8·5 cm. long, peduncle 1·8–2 cm. long, densely sericeous-tomentose; *fl.*: upper and lower receptacles densely sericeous-tomentose; calyx-lobes acuminate; style pilose. *Frt.* narrowly elliptic to oblong-elliptic, apex acute to obtuse, style frequently persistent, base acute to truncate, 5·5 × 2·4–7·5 × 3 cm., sericeous-tomentose; pedicel 0·5–0·8 cm. long.

T. albida shows no appreciable variation, the leaves remain more or less constant in shape, and there is no marked difference in size. The fruits are slightly variable in shape, but show no appreciable variation in size.

Gambia. No locality or date given, frt., *Dawe* 44 (K). Genieri, fl., frt., June 1949, *Fox* 83, 110 (K), medium-sized tree, common in the bush.

Portuguese Guinea. Catió between Néberem and Guébu, frt., June 1945, *Espírito Santo* 2077 (K), shrub or small tree 3–6 m. high, in sclerophyllous woodland.

French Guinea. Cercle de Mamou, between Ditinn and Labé, fl., Apr. 1905, *Chevalier* 12880 (K).

Sierra Leone. Kambia Dist., Bubuya, May 1948, *Adames* 172 (K), frequent in orchard-bush savannah, shrubby tree with fragrant fls. Koinadugu Dist., Worowaia, fl., Apr. 1911, *Lane-Poole* 29 (K), small tree, in savannah forest. Dist., unknown, Buyabuya, Wallia, fl., Mar. 1892, *Scott Elliot* 4269 (BM, isotype; K, holotype), tree 7 m. high, common on plateau. Bombali Dist., Mateboi F. R., Batkanu, frt., July 1951, *Small* 139 (K), not common, found in swamp zone of *Lophira lanceolata* bush type, heavily farmed and fired, tree 10–13 m. high with well-developed crown. Id., Batkanu, alt. 100 m., fl., Apr. 1914, *Thomas* 20a (K).

Taxonomic history

T. argyrophylla was based on *Scott Elliot* 4269! which is the type number of *T. albida* described six years earlier.

Distribution and ecology

T. albida is a strictly West African species and has a limited distribution, occurring in Sudan- and Guinea-zone vegetation at various sites in Gambia, Portuguese and French Guinea, and Sierra Leone.

Aubréville (4) records it as being fairly frequent in French Guinea between Kouroussa and Kankan, with isolated groups crossing the Macenta-Beyla area to Kankan, it also occurs in the French Sudan in small areas between Bougoumi and Sikasso. Other small areas occur in Casamance and Sine Saloum in Senegal.

According to Aubréville it is one of the first species to colonize cleared forest areas.

(24) **T. stenostachya** Engl. & Diels, *Monogr.* **4**, 16, t. 7 B (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 722 (1921); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.* **5** (Tang. Terr.), **2**, 144 (1949).

T. rhodesica R. E. Fries, *Wiss. Ergebn. Schwed. Rhod.-Kongo Exped.*, 1911–12, **1**, 172, t. 13 (1914); Engl., *op. cit.* 722 (1921), synon. nov.

Terminalia sp. Brenan, *Mem. N.Y. Bot. Gard.* **8**, 437 (1954).

T. torulosa auct. non F. Hoffm. sens. strict.; Engl. & Diels, *op. cit.* p. 15 (1900) pro parte quoad *Kirk* s.n. tantum.

See Fig. 24. Shrub, 4 m. high, or laxly-branched small tree, 5–12 m. high, occasionally to 20 m. high, crown spreading; bark of bole dark grey to black, rough, with deep longitudinal ridges and grooves producing a lattice-like effect; OB dark brown, thick, hard, IB pink, yellow towards inside, thick, very fibrous; bark of branchlets greyish brown, fibrous, later longitudinally fissured. Young shoots densely tomentose, becoming glabrous. *Lvs.* elliptic to oblong-elliptic, apex acute to rounded, base obtuse to rounded or narrowly subcordate, 11 × 4·6–17·8 × 5·4 (–7·5) cm., young leaves ± tomentose on both surfaces, later glabrous above except for midrib, sparsely pubescent beneath, eventually almost glabrous and somewhat glaucous, old leaves sometimes bullate above, slightly undulate, chartaceous; *upper surface*: midrib and secondary nerves ± impressed, tertiary nerves and venation inconspicuous (or obscurely impressed in old leaves); *lower surface*: midrib and secondary nerves prominent, tertiary nerves subprominent, venation conspicuous but

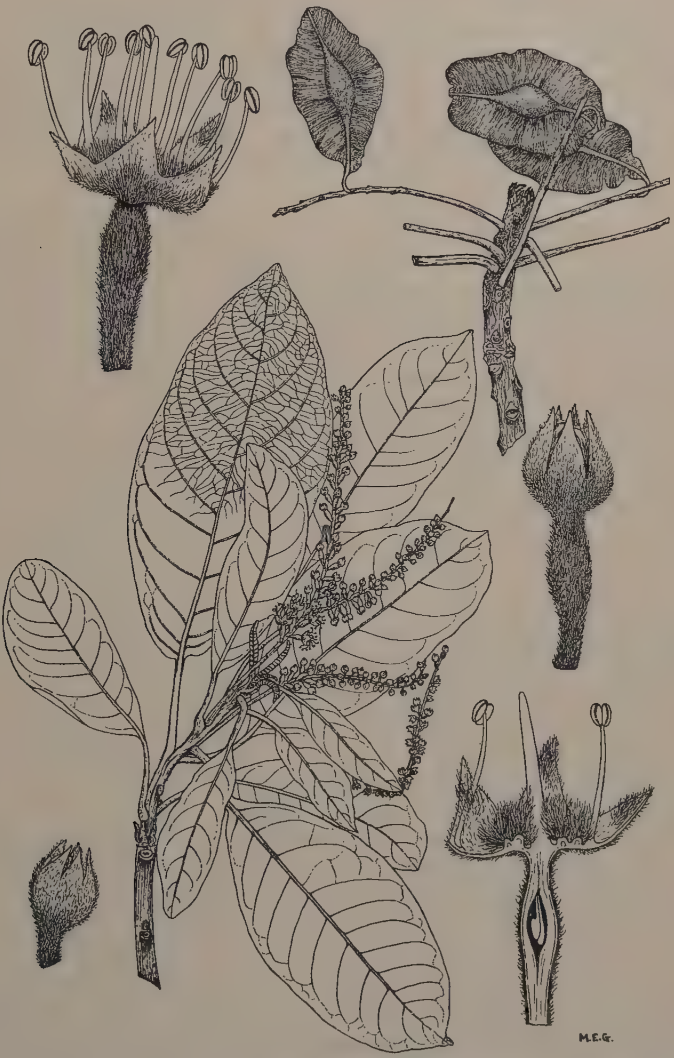

Fig. 24. *T. stenostachya* Engl. & Diels. Flowering specimen from *Clements* 137. Fruiting specimen from *White* 2256.

not raised; petiole 1·5–2·8 cm. long. *Infl.* (9–) 10·7–15·5 cm. long, peduncle 2·5–3·9 cm. long, tomentose; *fl.*: lower receptacle densely tomentose, upper receptacle sparsely pubescent; calyx-lobes acuminate. *Frt.* oblong to oblong-elliptic or narrowly elliptic, apex obtuse to rounded, base obtuse to subtruncate, 4·5 × 2·4–6·2 × 3 cm., minutely puberulous, reddish brown to yellowish red; pedicel 0·5–0·6 cm. long.

On the whole, leaf-shape remains fairly constant, but leaf-size varies considerably; the extreme size is in the region of 22 × 9 cm. (average size about 11 × 4·5 cm.). The amount of indumentum on the leaves varies (mainly) according to the stage of development, but in the fruiting stage the leaves may remain tomentose, or may be glabrous except for the main nerves beneath, or may be completely glabrous. The length of inflorescence varies markedly, occasionally attaining a length of 15·5 cm. The fruits are very variable, both in size and shape, varying in size from 3·5 × 1·7 cm. (exceptionally small) to nearly twice this size, and varying in shape from narrowly elliptic to oblong.

BELGIAN CONGO. Haut Katanga Dist., between Kuinfundu and Kienge, frt., Feb. 1940, *Bredo* 3954 (BR). Tanganyika Dist., nr. Albertville, frt., Apr. 1948, *Schmitz* 1587 (BR), in savannah woodland, medium-sized shrub or tree with drooping branches. Haut Katanga Dist., Kundelungu Mts. nr. Lukafu, frt., July 1948, *Schmitz* 1891 (BR), on stony soil half-way down slope, small tree with wide-spreading crown and fissured bark.

TANGANYIKA TERRITORY. Ruponda Dist., Nachingwea, alt. 600 m., frt., Feb. 1953, *B. Anderson* 838 (K), in *miombo* woodland, on sandy soil nr. foot of slope, tree 5 m. high with spreading crown, bark longitudinally furrowed, frt. red. Manyoni Dist., Manyoni, nr. kopje, alt. 1400 m., fl., Dec. 1932, *Burtt* 4588 (K), coarsely-barked tree to 20 m. high, in *Brachystegia–Isoberlinia* woodland. Korogwe Dist., Mnazi, alt. 600 m., fl., May 1939, *Gillman* 900 (EA, K), tree 4–7 m. high. Shinyanga Dist., Shinyanga, frt., Nov. 1938, *Koritschoner* 1969 (EA). Morogoro Dist., nr. Morogoro, alt. 540 m., fl., Feb. 1932, *Wallace* 359 (K), tree 7 m. high.

PORTUGUESE EAST AFRICA. Boror Dist., Namagoa, alt. 134 m., Nov. 1945 *Faulkner* 337 (EA, K), tree with rough bark and hard timber (flg. specimen of *Faulkner* 375). Id., frt., Mar.–Apr. 1945, *Faulkner* 375 (K). Ribáuè Dist., Ribáuè, alt. 650 m., fl., Dec. 1942, *Gomes e Sousa* 2309 (K), in open forest, common small tree, fls. melliferous, yellowish. Massingire Dist., foot of Moramballe (Morrumbala), frt., Mar. 1859, *Kirk* s.n. (K). Maniça Dist., between Mavita and Rutand, frt., Nov. 1948, *Mendonça* 3798 (K), small tree in *Brachystegia* woodland. Tete Dist., between Zóbuè and Tete, fl., Oct. 1943, *Torre* 6010 (BM, K), in deciduous forest, tree 4–8 m. high.

NYASALAND. Kota-Kota Dist., Chia area, alt. 480 m., frt., Sept. 1946, *Brass* 17551 (K), tree 10 m. high in woodlands of dry lake plain. No locality given, but probably Blantyre, fl., 1895, *Buchanan* 352 (BM, lectotype). Mlanje Dist., nr. Likabula Timber Depot, Mlanje, fl., Oct. 1929, *Clements* 137 (FHO). South Nyasa Dist., Fort Johnston, Cimwala, Cimbiya Hill, frt., June 1955, *Jackson* 1676 (FHO), in *Elephantorrhiza–Sterculia* association, small tree with grey and black, striated bark, and pink frt. North Nyasa Dist., Ifumbo, nr. Songwe R., alt. 700–1400 m., fl., *Lewis* 40 (FHO), on alluvial soils in *Brachystegia–Combretum* savannah woodland, tree 10 m. high with white fls.

SOUTHERN RHODESIA. Charter Dist., Featherstone, about 106 km. S.W. of Salisbury, alt. 1500 m., frt., Mar. 1937, *Cairns* 11/47 (FHO), on basalt formation. Umtali Dist., municipal sandquarry site, Darlington commonage, alt. 1200 m., fl., Nov. 1954, *Chase* 5327 (FHO), tree 6 m. high with rough bole, broad leaves and yellow, scented fls. Wankie Dist., Victoria Falls, frt., Feb. 1912, *Rogers* 5568 (BM, K, SRGH). Lomagundi Dist., Hunyani R., below Zambezi Escarpment, alt. 667 m., frt., May 1949, *Whellan* 409 (FHO, K, SRGH), common tree. Mtoko Dist., nr. Mudzi R., 80 km. E. of Mtoko, fl., Nov. 1950, *Whellan* 475 (FHO).

NORTHERN RHODESIA. Livingstone Dist., Victoria Falls, frt., July 1911, *Fries* 78, 78a

(UPS, syntypes of *T. rhodesica*). Mumbwa Dist., Mumbwa, fl., about 1912, *Mrs Macaulay* s.n. (K). Abercorn Dist., Mpulungu–Lake Tanganyika, by main road, about 2 km. from Mpulungu, alt. 900 m., frt., Mar. 1952, *Mrs Richards* 1403 (K), tall tree, leaves pale green, upper surface smooth, lower surface downy, frt. rose-pink. Livingstone Dist., Katombora, F.R., frt., Mar. 1952, *White* 2256 (FHO), growing with *Kirkia acuminata* on shallow soil overlying Karroo basalt; small tree 9 m. high, 0·3 m. dbh, branches crooked, widespreading; bark grey-black, deeply ridged and grooved producing lattice-like effect, OB 1 cm. thick, dark brown, IB 0·8 cm. thick, pale red shading to yellow towards inside, very fibrous, frt. red. Fort Jameson Dist., nr. Indian quarter, Fort Jameson township, frt., Apr. 1952, *White* 2466 (FHO), growing with *Afrormosia angolensis* and *Combretum zeyheri*, on deep red loam at foot of rocky slope covered with *Brachystegia* woodland; small tree 9 m. high, 0·28 m. dbh, bark dark brown, coarsely striated, OB 0·9 cm., thick, dark brown, hard, IB 1 cm. thick, pink outside, lemon yellow inside, fibrous, leaves bright mid-green above, grey-green beneath, frt. dark red.

Taxonomic history

T. hildebrandtii of Burtt Davy & Hoyle, *Check-Lists For. Trees & Shrubs Brit. Emp.* **2**, (Nyasaland Protectorate), 39 (1936)) is undoubtedly *T. stenostachya*, which is very common in Nyasaland. Numerous specimens collected mainly by Clements, of which *Clements* 137 is cited above, were mis-identified in FHO as *T. hildebrandtii*, and presumably the error in the Nyasaland *Check-List* arose from this source.

The name *T. rhodesica* has been wrongly applied to *T. mollis*. However, the type material of *T. rhodesica* is very distinct from *T. mollis* but matches that of *T. stenostachya* described about fourteen years earlier.

T. stenostachya was based on *Buchanan* 352 ! and *Buchanan* in Herb. Wood 6838 (both flowering) from Nyasaland. *T. rhodesica* was based on *Fries* 78 ! and 78 a ! (both fruiting) from Northern Rhodesia.

The following specimens—*Kirk* s.n. ! (cited by Engler and Diels under *T. torulosa*), *Clements* 137 !, *Trapnell* 1464 !, *Michelmore* 609 !, *Eyles* 6394 !, 7653 !, 8588 !, and *Pardy* 121/33 !—are cited under 'T. sp.' by Brenan in his account of the *Terminalia* species collected by the Vernay-Lang Expedition; they are all conspecific with *T. stenostachya*.

Distribution and ecology

T. stenostachya is widely distributed, with its northern limit in the Lake Province of Tanganyika and its southern limit in the Ndanga District of Southern Rhodesia. It occurs in the Lake and Central Provinces of Tanganyika, and in the eastern districts as far south as Lindi, and in the Tanganyika and Katanga Districts of the Belgian Congo; it is scattered in Northern Rhodesia from north to south—as far as the Victoria Falls; it is widely distributed in Nyasaland and Southern Rhodesia, and in the north-western parts of Portuguese East Africa.

It mostly occupies rather rocky sites in the *Acacia* savannah woodland region of north-eastern Tanganyika, in the *miombo* region of central Tanganyika, and in the *miombo* and *mopane* woodland regions of South Tropical Africa.

The species recorded from Nyasaland under the name of *T. hildebrandtii* by Willan (*Emp. For. J.* **19**, 61 (1940)) is probably *T. stenostachya*. He states that it is a typical tree of the lower escarpment and foothill forest zone found north of Karonga and southwards to Ncheu.

IMPERFECTLY KNOWN SPECIES CLOSELY RELATED TO *T. STENOSTACHYA*

T. mangela *De Wild. & Ledoux* (in De Wild., *Contrib. Fl. Katanga*, Suppl. **2**, 90 (1929)) based on *Verdick* 232 ! (fl.) from Lukafu in Haut Katanga District of Belgian Congo.

T. verdickii *De Wild. & Ledoux* (De Wild., *op. cit.* 92, based on *Verdick* 315! (fl.) from same locality.

They are probably conspecific with each other and differ from *T. stenostachya* in the secondary and tertiary nerves being scarcely raised beneath, and in the very finely reticulated venation.

White 2820 (frt.) from northern Nyasaland also belongs here and differs from *T. stenostachya* in the same characters.

(25) **T. gazensis** Bak. f., *J. Linn. Soc.* (*Bot.*), **40**, 69 (1911); Engl., *Pflanzenw. Afr.* **3** (**2**), 723 (1921); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, **2**, 145 (1954).

See Fig. 25. Small tree, 7–17 m. high; bark of bole dark brown, longitudinally fissured; bark of branchlets grey-brown, fibrous. Young shoots tomentellous, becoming glabrous.

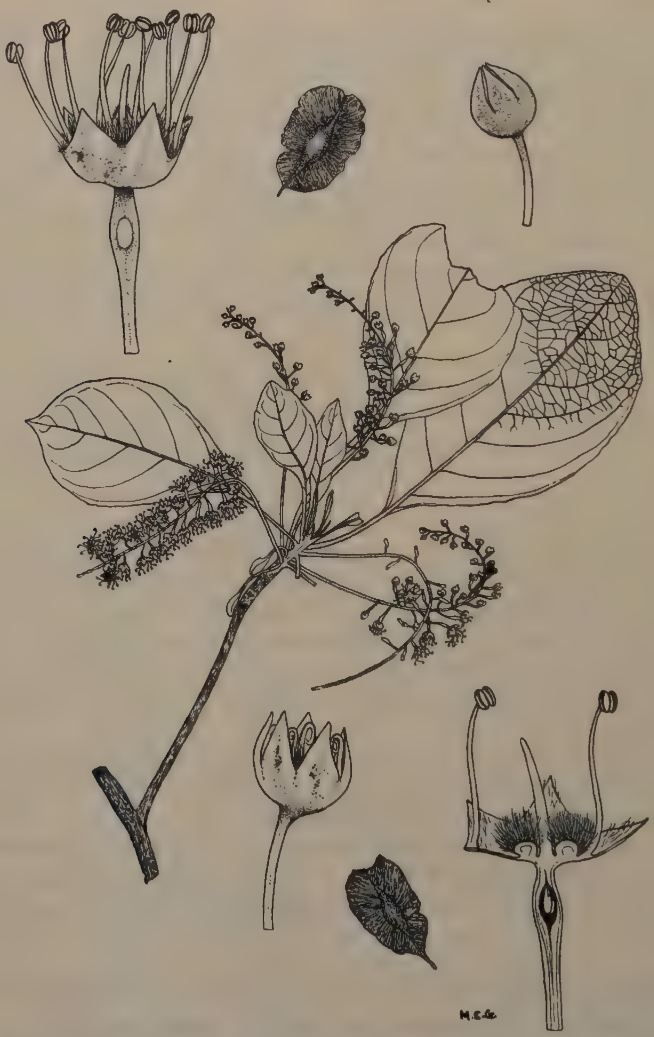

Fig. 25. *T. gazensis* Bak. f. Flowering specimen from *Hopkins* GH 13225. Fruits from *Mendonça* 3898.

Lvs. elliptic to elliptic-obovate, apex nearly always shortly acuminate, base acute, 9·5 × 4–14 × 6·5 cm., softly pilose or completely glabrous except for midrib above and petiole, usually repand-crenulate, thinly chartaceous; *upper surface*: midrib and secondary nerves slightly impressed, tertiary nerves and venation scarcely visible; *lower surface*: midrib prominent, secondary nerves subprominent, tertiary nerves and venation inconspicuous and not raised; petiole 2–2·5 cm. long. *Infl.* 7·5–8 cm. long, peduncle 2–3 cm. long, tomentose; *fl.* glabrous; calyx-lobes acute. *Frt.* oblong-elliptic, apex subtruncate, emarginate, base rounded to subtruncate, 2·5 × 1·7–3·0 × 2 cm., glabrous, greenish yellow; pedicel 0·4–0·5 cm. long.

The leaves show no appreciable variation in shape or size but vary in indumentum from densely pilose to subglabrous. Only two fruiting specimens are known, and these only show slight variation in the size and shape of the fruits. The inflorescence axis is consistently tomentose; the flowers consistently glabrous.

PORTUGUESE EAST AFRICA. Chimoio Dist., Mt. Garuso, fl., Jan. 1948, *Mendonça* 3584 (BM, K), in deciduous forest, tree 10–15 m. high; id., frt., Apr. 1948, *Mendonça* 3898 (BM, K), in residual forest; tree 8 m. high. Mossurize Dist., Zinyumbo Hills, alt. 500 m., Jan. 1907, *Swynnerton* 152a (BM, holotype), common throughout open veld of the lowlands, small tree with yellow fls. Kurumadzi R., alt. 700 m. fl., Nov. 1906, *Swynnerton* 596 (BM), tree with cream-coloured fls.

SOUTHERN RHODESIA. Umtali Dist., Commonage, alt. 1300 m., frt., June 1946, *Chase* GH no. 15085 (FHO, K), tree 17 m. high, bole similar to *T. sericea* but darker brown and more corrugated. Id., Christmas Pass, alt. 1340 m., fl., Jan. 1945, *Hopkins* GH no. 13225 (FHO, K), tree 10 m. high, with white fls. Melselter Dist., nr. Chirinda, fl., Jan. 1948, *McGregor* 15/48 (BM, FHO), in grassland, tree 7 m. high. Belingwe Dist., Ngobi Dip, nr. river, alt. 900 m., fl., Dec. 1953, *Wild* GH no. 44793 (FHO), tree 10 m. high with moderately rough, very dark bark and white fls. Selukwe Dist., Ferny Creek, by river, alt. 1000 m., fl., Dec. 1953, *Wild* GH no. 44833 (FHO), tree 13 m. high, bark moderately rough, grey.

Distribution and ecology

T. gazensis is confined to South Tropical Africa, occurring in the eastern districts of Southern Rhodesia and the Chimoio and Mossurize Districts of Portuguese East Africa. Little precise information is known about its ecology.

(26) **T. brownii** Fresen., *Mus. Senckenb.* **2**, 152, t. 9, fig. 1 (1837); A. Rich., *Tent. Fl. Abyss.*, **1**, 263 (1848); Laws., *Fl. Trop. Afr.* **2**, 415 (1871); Engl. & Diels, *Monogr.* **4**, 17, t. 8 A (1900); Engl., *Jahrb.* **39**, 513 (1907), incl. var. *gallaensis* Engl.; A. Chev., *Études Fl. Afr. Centr. Franç.* **1**, 119 (1913); Engl., *Pflanzenw. Afr.* **3** (**2**), 723 (1921), incl. var. *occidentalis* Engl.; *Aubrév., Fl. For. Soudano-Guinéenne*, p. 135 (1950); Eggeling, *Indigenous Trees Uganda Prot.* ed. 1, 47 (1940), Eggeling & Dale, ed. 2, 90 (1951); Keay, *Fl. West. Trop. Afr.* ed. 2, **1** (**1**), 279 (1954).

T. confertifolia Steud. ex A. Rich., *op. cit.* 263.
T. cycloptera R. Brown in Salt, *Abyss.* App. p. 64, nom. nud.
T. hemignosta Steud. ex A. Rich. pro syn. sub. *T. brownii* (op. cit.); ex Delile in Ferret & Galin., *Voy. Abyss.* **3**, 133 (1848).
T. semilikiensis De Wild., *Pl. Bequaert.* **4**, 346 (1928); Robyns, *Fl. Sperm. Parc Nat. Albert*, **1**, 666 (1948), synon nov.

See Fig. 26. Small tree, 7–13 m. high, occasionally to 25 m., high, rounded, spreading crown; bark of bole greyish, rough, longitudinally fissured; slash, dull red-brown; bark of branchlets grey, fibrous. Young shoots tomentose, becoming glabrous. *Lvs.* elliptic-obovate to broadly obovate, apex obtuse to shortly acuminate, base acute to obtuse, 8·5 × 3·8–12·5 × 6·5 cm., young leaves sericeous-tomentose, becoming softly pilose, later glabrous except for midrib above, remaining pilose beneath, occasionally repand, chartaceous; *upper surface*: midrib and secondary nerves ± impressed, tertiary nerves and venation slightly impressed; *lower surface*: midrib and secondary nerves prominent, tertiary nerves subprominent, venation conspicuous but not raised; petiole 1·5–2 cm. long. *Infl.* 9·5–11 cm. long, peduncle 1·5–2 cm. long, tomentose; *fl.* glabrous; calyx-lobes acuminate. *Frt.* broadly elliptic to ovate, apex obtuse to rounded, emarginate, base acute to obtuse, 3·5 × 2·2–4·2 (–5) × 2·5 cm., glabrous, purplish red to brown; pedicel 0·5–0·7 cm. long.

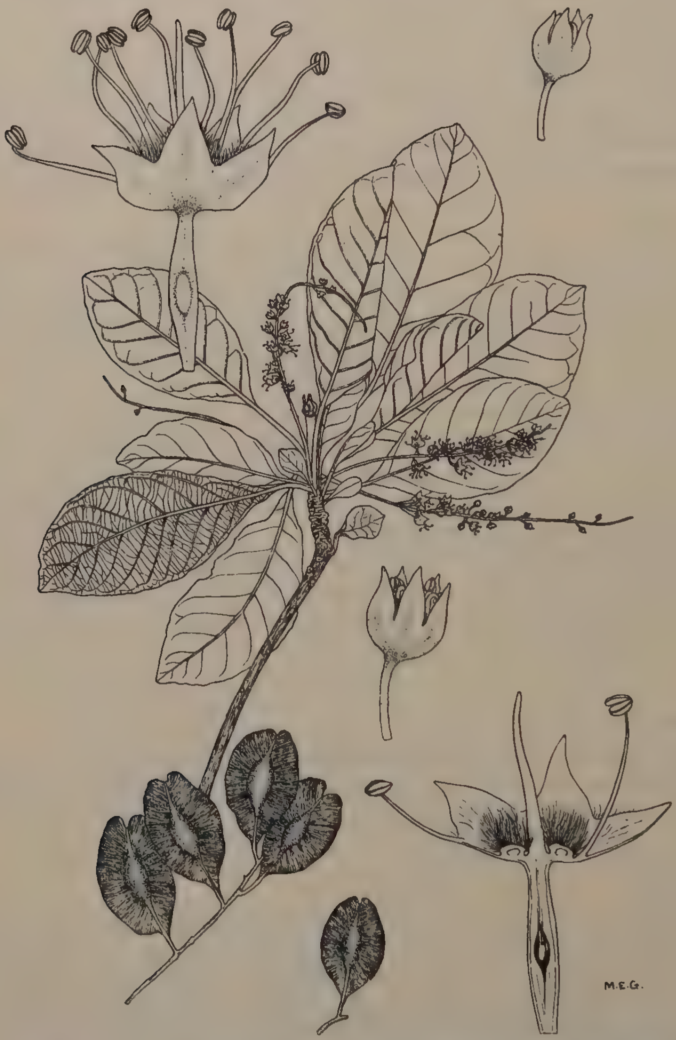

Fig. 26. *T. brownii* Fresen. Flowering specimen from *Wigg* 1427. Fruiting specimen from *Greenway* 7873.

The leaves show fairly considerable variation in size and shape, frequently on the same specimen. The fruits show marked differences in shape and quite appreciable variation in size, but very rarely exceed about 5 cm. in length. The inflorescence axis is consistently tomentose; the flowers consistently glabrous.*

NIGERIA. Bornu Div., hills nr. Kilba country on Bornu Rd., frt., July 1909, *Dalziel* 94 (K). Bauchi Div., Bauchi Plateau, frt., Aug. 1930, *Lely* P628 (FHO, K), on rocky ground, tree 13 m. high with purple frt.

BELGIAN CONGO. Kibale Ituri–Kivu Dist., Kasonsero, Semliki Valley, fl., young frt., July 1914, *Bequaert* 5050 (BR, holotype of *T. semlikiensis*), in gravel ravine, small twisted tree with white fls. Kibali Ituri Dist., Bogoro escarpment, fl., May 1949, *De Craene* 255 (BR), small tree, 4–5 m. high, with open crown and yellow fls. Id., Mahagi Port, frt., Nov. 1937, *Di. For.* 605 (BR), tree 10 m. high, 0·4 m. diam., of irregular form, bark deeply fissured, grey.

ERITREA. On rocky hillside, S. foot of Asciorum Pass, alt. 940 m., frt., Mar. 1949, *Bally* 6820 (K), not common, tree 7 m. high. Escarpment below Ghinda, alt. 1000 m., frt., May 1949, *Bally* 7102 (K), common tree with spreading crown and purplish red frt. Keren, Abita, Mt. Deban, alt. 1500–1640 m., fl., June 1870, *Beccari* 88 (K). Keren, fl., frt., Sept. 1861, *Steudner* 194 (K). Atirba, fl., Sept. 1861, *Steudner* 198 (K).

ETHIOPIA. E. of Harar, frt., Apr. 1943, *Lieut. Hummell* 59 (EA, K), large savannah tree with spreading crown. Berrethowa, fl., frt., Sept. 1862, *Schimper* 134 (BM), medium-sized tree, common in mountainous Kolla country up to 1730 m. alt. Nr. foot of Sabra Mt., frt., July 1842, *Schimper* 583 (BM, CGE, K, OXF), tree or shrub. High ground along Takkaze R., frt., Nov. 1839, *Schimper* 722 (CGE, K, OXF), tree. Between Dschelad-scheranne and high ground along Takkaze R., fl., Jan. 1840, *Schimper* 879 (BM, K, OXF), isotypes of *T. hemignosta*, medium-sized tree.

BRITISH SOMALILAND. Nr. Mandera, about 51 km. W. of Upper Sheikh, fl., Mar. 1950, *Dawson* 3 (K). Duwi, about 64 km. N. of Hargeisa, alt. 1000–1200 m., fl., frt., Oct. 1932, *Gillett* 4424 (EA, K), in *Acacia*–open grass community, on northern slopes, dominant in parts, tree 5 m. high. Sheikh area, at foothills of Waggar Range, st., Dec. 1944, *Glover & Gilliland* 466 (FHO, K), occasional tree in gulleys. On seaward slopes of Waggar Range, frt., Feb. 1945, *Glover & Gilliland* 802 (EA, FHO, K), large tree 25 m. high, bark ridged. Gan Libah, on Golis Range, alt. 1400 m., fl., July 1945, *Glover & Gilliland* 1208 (EA, FHO, K), locally frequent on escarpment, tree up to 6 m. high.

SUDAN REPUBLIC. Kassala Prov., Has Has, Karora Hills, nr Eritrean border, fl., Feb. 1923, *Crowfoot* s.n. (K). Milbes nr. Choor R., frt., Nov. 1839, *Kotschy* 280 (BM, OXF). Darfur Prov., Jebel Marra, alt. 1700 m., fl., Apr. 1920, *Lynes* s.n. (BM), by the cascade, conspicuous little tree. Kordofan Prov., El Obeid, frt., July 1875, *Pfund* 148 (K). Id., Birket-Kolli, fl., July 1875, *Pfund* 149 (K).

UGANDA. Mubende Dist., Lake Albert, nr. mouth of Muzizi R., alt. 270–300 m., fl., Dec. 1906, *Bagshawe* 1319 (BM), common at foot of and on slope of escarpment, tree with white fls. Karamoja Dist., escarpment between Karamoja and Turkana, fl., frt., Feb. 1937, *Brasnett* 85 (EA, FHO), in stony river-bed, tree 7 m. high, bark rough, channelled, dark. West Nile Dist., Moyo, in the Rudu or grove sacred to the rainmakers, alt. 1270 m., frt., Dec. 1931, *Brasnett* 326 (K), common throughout Madi Dist. except in the almost treeless region, medium-sized tree, bark ± smooth, dark grey, with small vertical lines, slash yellow. Acholi Dist., Amiel, nr. summit of Kitela rock, alt. 1300 m., fl., frt., July 1946, *Dawkins* 189 (EA, FHO), in well-sheltered hollow containing, probably, deep sandy soil over granite; erect straight-boled tree to 10 m., bark grey, shallowly fissured, slash dull yellow, leaves dark green above, glaucous beneath, frt. deep pink, greenish on sheltered side. Mbale Dist., Buligenyi, about 32 km. N.E. of Mbale, alt. 1530 m., frt., Aug. 1932, *Thomas* 393 (K), in grassland scrub, frequent, tree 10 m. high, leaves dark green, frt. purple.

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* The geographical ranges of *T. brownii* and *T. kilimandscharica* overlap only in northern Tanganyika and southern Kenya. Outside the region of overlap the two species are readily separated by the characters given in the key and by fruit shape (see figs. 26 and 27). Where they occur together, intermediates (e.g. *Greenway* 4492, *Hughes* 200 and *Rammell* 1245) have been collected. (F.W.)

KENYA. Trans-Nzoia Dist., Elgeyo escarpment, alt. 2000 m., frt., Jan. 1934, *Dale* 3199 (BM, EA, FHO, K). Id., Aug. 1934, *Dale* 3258 (EA), flowering specimen of *Dale* 3199. Northern Frontier Dist., Dandu, alt. 900 m., frt., Mar. 1952, fl. May 1952, *Gillett* 12580 (K), on granite mountain, tree 10 m. high, fls. cream, frt. purplish red. Id., Moyale, alt. 1400 m., frt., Apr. 1952, *Gillett* 12931 (K), in scrub, tree 10 m. high. S. Kavirondo Dist., 5 km. E. of Kendu Port, alt. 1300 m., frt., Aug. 1946, *Greenway* 7873 (EA, FHO, K), common, but scattered, with *Combretum collinum* on rocky granite outcrops, in a very gritty reddish pink sandy loam, amongst native millet, cotton and ground-nut cultivations; a much-branched tree to 13 m. high, round crown, bark rough, greyish black, frt. purplish red. Baringo Dist., Marop, Kamasia, fl., Apr. 1941, *Wimbush* 1218 (EA, FHO), small tree 10 m. high with cream fls.

TANGANYIKA TERRITORY. Moshi Dist., Moshi township, fl., May 1935, *Davies* 1031 (EA, K), common tree. Dodoma Dist., Gulwe, alt. 1000 m., fl., frt., Nov. 1931, *Hornby* 396 (EA, K), on red clay soil, common tree to 13 m., with small white fls. Moshi Dist., Rau Forest, alt. 800 m., fl., Nov. 1924, *Lewis* 240 (K), small tree. Moshi Dist., Moshi township, alt. 1000 m., fl., Nov. 1938, *Wigg* FH 1427 (EA, FHO), in savannah, medium-sized tree, bark lenticularly reticulated, fls. yellow, young frt. crimson.

Taxonomic history

Fresenius based *T. brownii* on *Rüppell* s.n. (not seen), collected between Temben and Simen, and regarded *T. cycloptera* R. Br., nom. nud., as a synonym.

T. confertifolia was based on a flowering specimen—*Schimper* 817 (not seen) collected in Ethiopia. Steudel used the name on the printed label on Schimper's specimen, and it was described by Richard (*Tent. Fl. Abyss.* **1**, 263 (1848)), who states that it differs from *T. brownii* in the obovate leaves, which are glabrous, except for the nerves on the lower surface. The leaves certainly come within the range of variation of *T. brownii.*

The name *T. hemignosta*, based on *Schimper* 879! (fl.) also from Abyssinia, was provided by Steudel as a nomen nudum. It is included under *T. brownii* by Richard (*op. cit.*). It has densely pilose leaves (on lower surface) and these again come within the range of variation of *T. brownii.*

T. cycloptera (R. Brown in Salt, *Abyss.*) has not been seen; it is accepted as a synonym of *T. brownii* by Lawson (*Flor. Trop. Afr.* **2**, 415 (1871)) and by Engler and Diels in their monograph.

T. semilikiensis was based on *Bequaert* 5050! (fl., young frt.) from the Semliki Valley along the Belgian Congo–Uganda border. It has slightly narrower leaves than usual but is definitely conspecific with *T. brownii.*

Distribution and ecology

T. brownii is widespread throughout East Tropical Africa from the Kassala Province of Sudan Republic to the Central Province of Tanganyika; it has a western outlier on the Bauchi Plateau in Nigeria.

In Nigeria it occurs in the Guinea zone, and according to Aubréville (3 and 4) is found in those parts of the north-western Cameroons that are occupied by a xerophilous montane bush type of vegetation.

In the Sudan Republic (34) it is a common species in the *Acacia*–short-grass community (with *A. mellifera* typically present) which occurs in a strip across Darfur and Kordofan to Kassala and the coast. It frequently occurs with *Adansonia digitata* on sites receiving a water supply in addition to the normal annual rainfall. It also occurs on the Jur River flood plains with 800 mm. (32 in.) annual rainfall, on sands in the Nahud area with 500 mm. (20 in.) p.a., and in various rocky valleys such as on Jebel Daier with 400 mm. (16 in.).

According to Logan (23) *T. brownii* is common in central and southern Ethiopia, and occurs with *Combretum molle*, *Acacia albida* and *A. seyal* in a dry type of savannah woodland, occupying sites on the lower and middle slopes of plateau escarpments and sometimes on the plateaux themselves. In most areas this type lies between the upper-montane rain-forest or high-montane Conifer forest and the thornlands of the lowlands. *Combretum molle*, *Bauhinia* sp. and *T. brownii* are among the first of the species of the dry savannah to appear in the transition from rain forest to 'orchard' country.

In British Somaliland (14) *T. brownii* is common on the lower slopes of Ogo Plateau, and, in the Haud, in an *Acacia bussei* association belonging to the tree-*Acacia* open woodland type of vegetation. It also forms part of the *A. glaucophylla*–*A. etbaica*–*T. brownii*–*Dracaena schizantha* association found on the northern slopes of the coastal mountains above the *Commiphora*, bush-*Acacia* open scrub, where these mountains are not occupied by evergreen scrub or *Juniperus* forest. *T. brownii* forms one of the dominant species on non-limestone rocks. It occurs in the transition from tree-*Acacia* open woodland to *Commiphora*, bush-*Acacia* open scrub. It is also found as a constituent of a deciduous scrub community occurring to the south and south-east of Harar in eastern Abyssinia, where the dry season is shorter and the rainfall rather higher than in the above areas. It also occurs, as scattered trees, in an evergreen scrub type in Harar District; where the local dominants are *Acokanthera schimperi* and *Cadia purpurea*.

T. brownii is common in the lower-montane woodland area along the Congo–Uganda border, and, according to Lebrun (21), occurs sporadically in pure stands in the Semliki Basin. It appears to be a common species in this vegetation type, which also occupies large areas in Uganda and some western parts of Kenya. In the latter territory it extends to the south-east into the drier *Acacia* savannah, and northwards to Dandu and Moyale, where the vegetation is of a similar type.

In the Karamoja District of Uganda (36) *T. brownii* is very common with *Acacia albida* in fringing forest, and on top of escarpments with *Combretum molle*. It is also found in the *Acacia* thickets and woodlands of the east, which occupy an area south from Moroto and east from Kadam to the south-east corner of the district. Thomas (36) states that species such as *T. brownii* and *Combretum molle* are more abundant in deciduous woodland, and suggests that they may be relics. *T. brownii* is also found in deciduous scrub on eluvial and alluvial soils around Moroto, Lorengidwat and Kodunyo (11).

In Tanganyika it occupies sites in the *Acacia* savannah type, as in Kenya, and does not appear to penetrate into the *miombo* woodland region farther south.

(27) **T. kilimandscharica** Engl., *Pflanzenw. Ost-Afr.* C, 294 (1895); Engl. & Diels, *Monogr.* **4**, 19, t, 9 B (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 723 (1921); Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.*, **5** (Tang. Terr.), **2**, 145 (1949).

T. hildebrandtii Engl., *op. cit.* 294 (1895); Engl. & Diels, *op. cit.* 19, t. 9 C (1900); Engl., *op. cit.* 723 (1921); Brenan & Greenway, *op. cit.* 145, synon. nov.

T. sambesiaca Engl. & Diels, *op. cit.* 13, t. 4 A (1900); Schinz, *Pl. Menyhart. Denkschr. Akad. Wiss. Wien.* **78**, 431 (1905); Engl., *op. cit.* 721 (1921); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, **2**, 145 (1954), synon. nov.

T. aemula Diels in Engl., *Jahrb.* **39**, 511 (1907); Engl. *op. cit.* 721 (1921); Brenan & Greenway, *op. cit.* 143; Mendonça, *op. cit.* 145, synon. nov.

T. brownii auct. non Fresen.; Brenan & Greenway, *Check-Lists For. Trees & Shrubs Brit. Emp.*, **5** (Tang. Terr.), **2**, 144 (1949) pro parte quoad *Greenway* 4453 & 4492 tantum.

See Fig. 27. Small or medium-sized tree, 7–20 m. high, occasionally to 40 m. high, spreading crown and fairly straight trunk; bark of bole greyish, rough, longitudinally fissured; bark of branchlets grey-brown, fibrous. Young shoots tomentose, becoming glabrous. *Lvs.* elliptic-obovate to broadly obovate, apex obtuse to shortly acuminate, base acute to obtuse, 9 × 3·8–14 × 6 cm., softly pilose becoming glabrous, occasionally repand, chartaceous; *upper surface*: midrib and secondary nerves ± impressed, tertiary nerves and venation slightly impressed; *lower surface*: midrib and secondary nerves prominent, tertiary nerves subprominent, venation conspicuous but not raised; petiole 1·5–2·5 cm. long. *Infl.* 9·5–12·5 cm. long, peduncle 1·5–2 cm. long, tomentose; *fl.*: lower

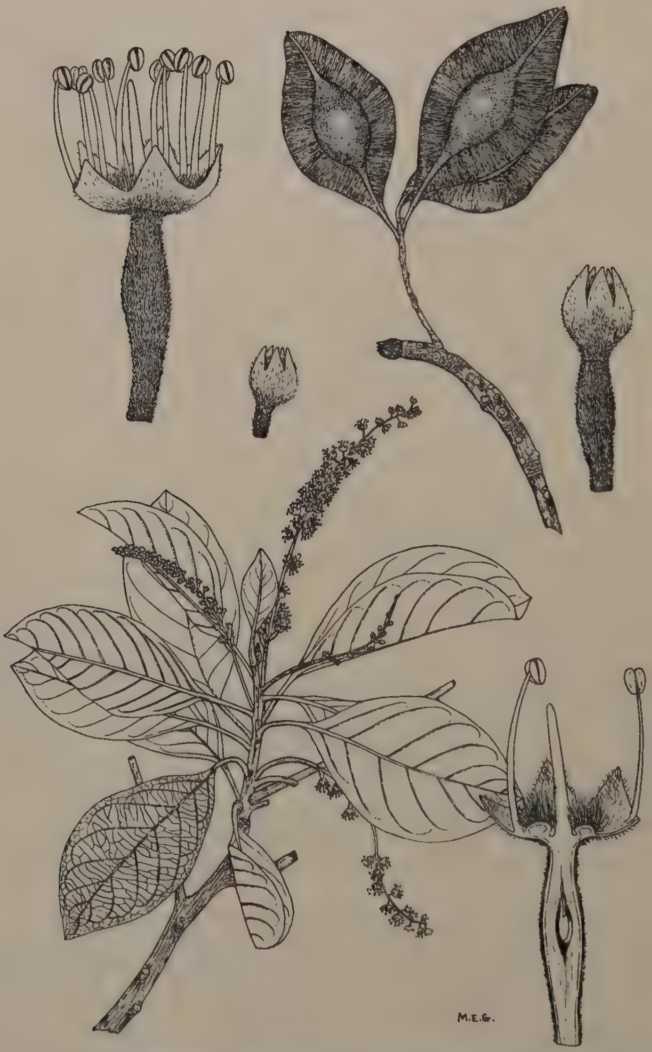

Fig. 27. *T. kilimandscharica* Engl. Flowering specimen from *Greenway* 4453. Fruiting specimen from *Menyhart* 613.

receptacle densely tomentose, upper receptacle sparsely pubescent; calyx-lobes acute. *Frt.* broadly elliptic to oblong-elliptic, tapering from the middle rapidly to both ends, apex acute to obtuse, emarginate, base acute to obtuse, (6 –) 7 × 3·5–8·5 × 3·8 cm., minutely puberulous to almost glabrous but a few hairs usually persisting even when mature, brownish red; pedicel 0·7–0·8 cm. long.

Leaf-shape remains fairly constant, and on the whole there is no appreciable variation in leaf-size except in some of the Southern Rhodesian material, in which size may vary from 15 × 6 cm. to 20·5 × 9·5 cm. on the same specimen. The indumentum on the mature leaves varies from densely pilose to subglabrous even on flowering specimens, but usually the leaves become almost glabrous by the time the fruits attain maturity. The fruits vary considerably in size and shape, but are very rarely smaller than 6 × 3·8 cm.

KENYA. Northern Frontier Dist., Ngare–Narok, Matthew's Range, alt. 1700 m., frt., Apr. 1944, *Mrs Joy Bally* 56 (K). Kilifi Dist., Marafa, about 25 km. N.W. of Mambrui, alt. 130 m., fl., Jan. 1937, *Dale* 3649 (BM, EA, K), in cultivated land nr. the coast, tree 8 m. high. Lamu Dist., nr. Witu, fl., *Elliot* 211 (FHO). Machakos Dist., Kibwesi, Ukambani, alt. 1000 m., frt., June 1906, *Scheffler* 174 (BM, K), tree 8–12 m. high. Id., Garabani Hill, nr. Sultan Hamud and Emali, alt. 1640 m., frt., Mar. 1940, *van Someren* 11 (FHO, K), large tree up to 10 m. high with spreading crown and fairly straight trunk.

TANGANYIKA TERRITORY. Pare Dist., above Makania, alt. 1100 m., fl., frt., Jan. 1945, *Bally* 4246 (K), common tree, frt. red-wine-coloured. Kondoa Dist., on rocky hills above Kondoa, alt. 1700 m., fl., frt., Mar. 1928, *Burtt* 1613 (BM, EA, K). Moshi Dist., Lake Chala, alt. 1200 m., fl., Jan. 1936, *Greenway* 4453 (EA, FHO), in *Acacia–Lannea–Pappea* association on dark brown volcanic soil, not very common, much-branched tree up to 7 m. high. Id., on lower slopes of Kilimanjaro, alt. 700–1000 m., fl., Oct. 1884, *H. Johnston* s.n. (BM, isotype; K, holotype). Lindi Dist., between Lindi and Lake Lutamba, about 40 km. W. of Lindi, alt. 200–250 m., fl., Nov. 1934, *Schlieben* 5630 (BM), in open woodland, tree 20 m. high.

PORTUGUESE EAST AFRICA. Tete Dist., Mfidzi R., nr. Boroma, frt., Apr. 1892, *Menyhart* 613 (Z, holotype of *T. sambesiaca*), tree 25 m. high.

NYASALAND. Dedza Dist., Mua Livulezi F. R., frt. Dec. 1953, *Adlard* 20 (FHO).

SOUTHERN RHODESIA. Umtali Dist., Laurenceville, alt. 1400 m., fl., Dec. 1952, *Chase* GH no. 41855 (FHO). Urungwe Dist., on rocky outcrop nr. Cheware R., fl., Dec. 1952, *Lovemore* GH no. 40951 (FHO), tree 5 m. high with grey, slightly rough bark and white fls.

Taxonomic history

The names *T. hildebrandtii* and *T. aemula* have been indiscriminately applied to any specimen which differed from *T. brownii* in having larger fruits or a tomentose inflorescence.

T. hildebrandtii was based on *Hildebrandt* 2832 (frt.) from Kitui in the Ukamba region of Kenya, and *Hildebrandt* 2367 (frt.) collected between Duruma and Teita further south, also in Kenya. *T. aemula* was based on *Engler* 3447 (frt.) from Amani in Tanganyika. *T. sambesiaca* was based on *Menyhart* 613! (frt.) from Boruma in Portuguese East Africa. *T. kilimandscharica* was based on *Johnston* s.n.! (fl.) from the lower slopes of Mt. Kilimanjaro.

The type material of *T. hildebrandtii* and *T. aemula* has not been seen, but judging by the original descriptions, they are conspecific with *T. kilimandscharica*. In the case of *T. aemula* a duplicate of *Scheffler* 174! was sent from Berlin to Kew under this name, and is certainly conspecific with *T. kilimandscharica*.

T. sambesiaca only differs from *T. kilimandscharica* in the subglabrous leaves; however, the leaves of the latter frequently become almost glabrous by the time the fruits attain maturity.

The name *T. kilimandscharica* is maintained rather than that of *T. hildebrandtii*; they were both described at the same time, but the type specimen of the former is available, whereas the type of the latter was destroyed in Berlin during the war.

Distribution and ecology

T. kilimandscharica has a discontinuous distribution from the Northern Frontier District of Kenya, through the southern and coastal districts of this territory, to the Western, Central and Tanga Provinces of Tanganyika; it occurs again at Tete in Portuguese East Africa and reaches its southern limit in the Umtali District of Southern Rhodesia. It occurs in a wide range of vegetation types, from the fine-leaved *Acacia* desert-grass savannah region of Kenya and the coastal savannah containing patches of evergreen thicket and forest, also in Kenya; to the *miombo* woodland areas of Tanganyika and Southern Rhodesia, and the regions of *mopane* woodland found around Tete and in the northern parts of Southern Rhodesia.

(28) **T. phanerophlebia** Engl. & Diels, *Monogr.* **4**, 19, t. 12 C (1900); Engl., *Pflanzenw. Afr.* **3** (**2**), 723 (1921); Burtt Davy, *Man. Fl. Trees Shrubs Transv.* **1**, 249 (1926); Mendonça, *Estudos, Ensaios Documentos*, **12**, *Contrib. Fl. Moçambique*, **2**, 146 (1954).

See Fig. 28. Shrub, about 3 m. high, or small tree, 7 m. high; bark of branchlets finely striated, grey-brown. Young shoots with scattered appressed hairs, becoming glabrous. *Lvs.* obovate, narrowed from above the middle to the base, apex shortly acuminate, sometimes rounded and emarginate, base acute, 3 × 1·5–10·5 × 4·5 cm., appressed-pilose on main nerves, otherwise sparsely pilose to glabrous, sometimes serrated, chartaceous; *upper surface*: midrib flattened or slightly impressed, secondary and tertiary nerves and venation conspicuously impressed; *lower surface*: midrib and secondary nerves prominent, tertiary nerves subprominent, venation conspicuous but not raised; petiole 0·3–1·8 cm. long. *Infl.* 8·5–9·5 cm. long, peduncle 1·5–1·8 cm. long, tomentose; *fl.*: lower receptacle densely tomentose, upper receptacle sparsely pubescent at base only; calyx-lobes obtuse. *Frt.* broadly elliptic-oblong, apex acute to rounded to truncate, base subtruncate, 2·8 × 1·8–4 × 2·7 cm., minutely puberulous, greenish yellow; pedicel 0·2–0·3 cm. long.

There is no appreciable variation in leaf-shape, the leaves remaining essentially obovate. Leaf-size varies considerably, as can be seen by the above measurements. The serrated margin is not a constant character, but usually at least some of the leaves on a specimen show it. The fruits remain more or less the same shape and show no marked variation in size.

PORTUGUESE EAST AFRICA. Magude Dist., Mapulanguene, along Uanetze R., fl., Nov. 1944, *Mendonça* 3181 (BM, K), shrub to 3 m. high on rocky ground. Sabi Dist., on small hills between Boane and Moamba, fl., frt., Dec. 1944, *Torre* 6861 (BM, K), small tree on stony ground in deciduous woodland.

PORTUGUESE EAST AFRICA or TRANSVAAL. Libombo Mts., frt., Jan. 1929, *Pole Evans* s.n. (BM).

TRANSVAAL. Barberton Dist., 5 km. N. of Malelane, alt. 340 m., fl., frt., Feb. 1949, *Codd* 5235 (BM, FHO, K, SRGH), in low veld bush in stony watercourse, tree 7 m. high with rough green leaves and white fls. Pilgrims Rest Dist., Eileen Orpen Dam, nr. Tshokwane, alt. 300 m., frt., Aug. 1950, *Codd* 6140 (K), on rocky slopes, sparsely branched shrub 1·5 m. high. Lydenberg Dist., 10 km. S.W. of Penge Mine, alt. 1000 m., frt., June 1954, *Codd* 8790 (K), on steep rocky hillside, small tree 3·5 m. high. Barberton Dist., Honeybird Creek, alt. 600 m., frt., Mar.–Apr. 1890, *Galpin* 884 (K, lectotype), shrub 3 m. high. Id., Komatipoort, alt. 33 m., fl., Dec. 1897, *Schlechter* 11743 (BM, K, paratype).

SWAZILAND. Mbabane Dist., Harman's Farm, on Hlotyo Stream, alt. 700 m., fl., Dec. 1939, *O. B. Miller* S/184 (FHO), tree 5 m. high.

NATAL. Babanango Dist., Umfolosi Causeway, fl., Jan. 1946, *Acocks* 12316 (K).

Distribution and ecology

T. phanerophlebia is a strictly South African species occurring in eastern Transvaal, Swaziland and northern Natal; it extends to the extreme southern part of Portuguese East Africa. It occupies areas in the low veld region, and according to Codd (7) is not very common at any of its localities in the Transvaal.

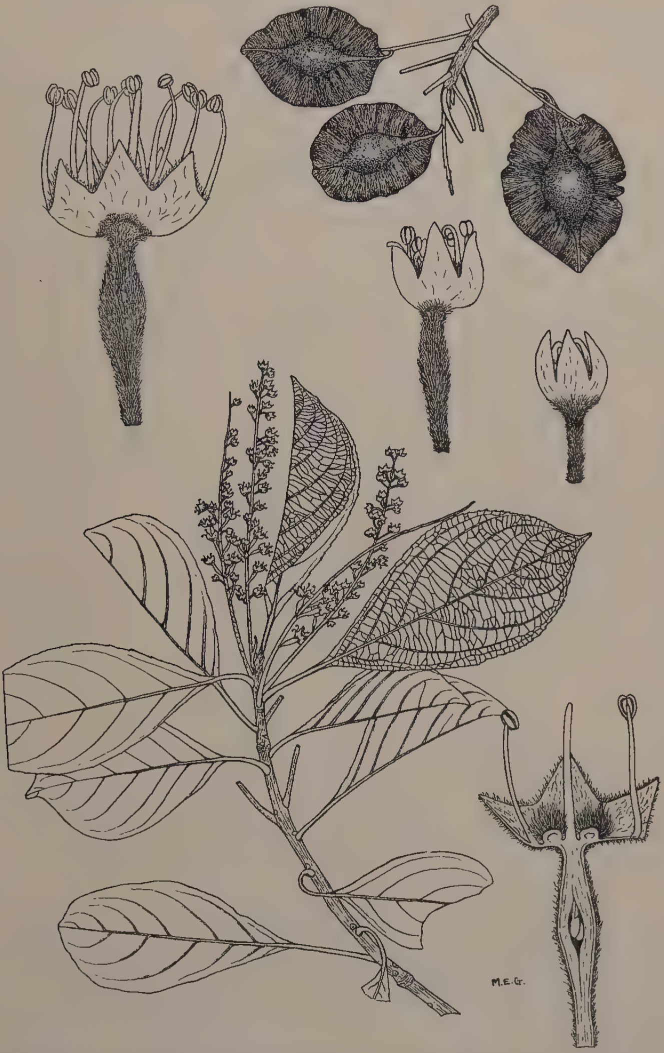

Fig. 28. *T. phanerophlebia* Engl. & Diels. Flowering and fruiting specimens from *Codd* 5235.

IV. Distribution and ecology of the African species

The distributions of twenty-four of the species of *Terminalia*, treated at length in this work, are shown on the map (Fig. 29), in relation to the regional vegetation zones of Tropical Africa. The distributions are based exclusively on the herbarium material examined. For some areas, especially the Ubangi Shari region and Abyssinia, very little material is available, and this should be borne in mind when interpreting the distributions shown.

The limits of rain-forest and the 20 in. (500 mm.) isohyet are taken from White (38). The rain-forest region (as marked on the map) includes the wet rain-forest and the mixed deciduous or dry rain-forest of English authors; the boundary roughly corresponds to the 50 in. (1250 mm.) isohyet, and between it and the 20 in. isohyet lies the broad-leaved savannah woodland zone; outside the latter is the microphyllous woodland, semi-desert and desert vegetation. In southern Africa the 10 in. (250 mm.) isohyet (taken from the most up-to-date rainfall map available) is also marked; this demarcates the large Karroo region and the deserts and semi-deserts of South-west Africa.

One species (*T. scutifera*) is confined to coastal habitats in West Africa, and another (*T. fatraea*) has a coastal distribution in East Africa. Two species (*T. superba* and *T. ivorensis*) are confined to the rain-forest region; *T. glaucescens* sometimes occurs in the dry deciduous forest, but is more often found in the broad-leaved savannah woodland. All the other species occurring within the rain-forest region occupy derived-savannah sites, and are more characteristic of the broad-leaved woodland zone.

The genus has its greatest concentration of species in the broad-leaved woodland zone. Of the seven species occurring in this zone in West Africa, only two (*T. mollis* and *T. brownii*) also occur south of the equator. The greatest concentration of species occurs in East Africa from Eritrea to the northern Transvaal. Some species (for example, *T. sericea*) have extensive distributions; others (for example, *T. randii* are much more restricted).

In West Africa, the genus scarcely extends north of the 20 in. isohyet, and no species is restricted to these drier regions. In north-eastern Tropical Africa, about six species are widely distributed in the drier areas, and have their centres of distribution there; some (for example *T. polycarpa* and *T. parvula*) are confined to this region. South of the equator, two species (*T. sericea* and *T. prunioides*) play an important part in the vegetation of drier areas with less than 20 in. annual rainfall, but also occur in regions with a higher rainfall.

So far as is known, no species are confined to the East African coastal forests, but the latter have been largely destroyed by man, and a number of species (for example, *T. spinosa*) have invaded the resulting derived savannah, from the adjoining zone.

V. Species introduced into Africa

Terminalia catappa L. (Sect. **Eucatappa** Engl. & Diels)

Apparently a native of the sandy coasts of Malaysia and the Andamans, although there seems to be some doubt as to its precise country of origin. It is frequently planted in avenues as a shade tree, for which it is suitable because of the very regular shape. It sheds its leaves all at once, quite suddenly, usually twice a year, and unlike most tropical trees the leaves turn first yellow, then vivid red, before falling.

The timber is reddish and of good quality, and is used for building purposes. The kernal of the fruit is edible and contains a colourless fatty oil similar to almond oil. The bark and leaves are used for tanning leather, and the tannin in the bark is used for medicinal purposes.

It is planted throughout India, Burma, Northern Australia and Polynesia, South and Central America and Florida, the West Indies, and in Tropical Africa from Senegal to Tanganyika, Angola and Portuguese East Africa—in fact, it is planted in nearly all tropical countries.

T. bellirica (Gaertn.) Roxb. (Sect. **Belliricae** Engl. & Diels)

Occurs in deciduous monsoon forests and rain forests in India, Burma, Indo-China, Siam and Malaysia (Malay Peninsula, Sumatra, Java, North Borneo, Lesser Sunda Island, Central Celebes and Moluccas). It is cultivated at Amani in Tanganyika, and in the Botanical Gardens at Entebbe, Uganda.

The fruit is one of the commercial Myrobalans used for tanning leather, for black dye (together with sulphate of iron) to economize in the use of indigo, and for making ink. The trade name for the timber is 'Barbera', and it is used for house-building, after being steeped in water, which is said to make it more durable.

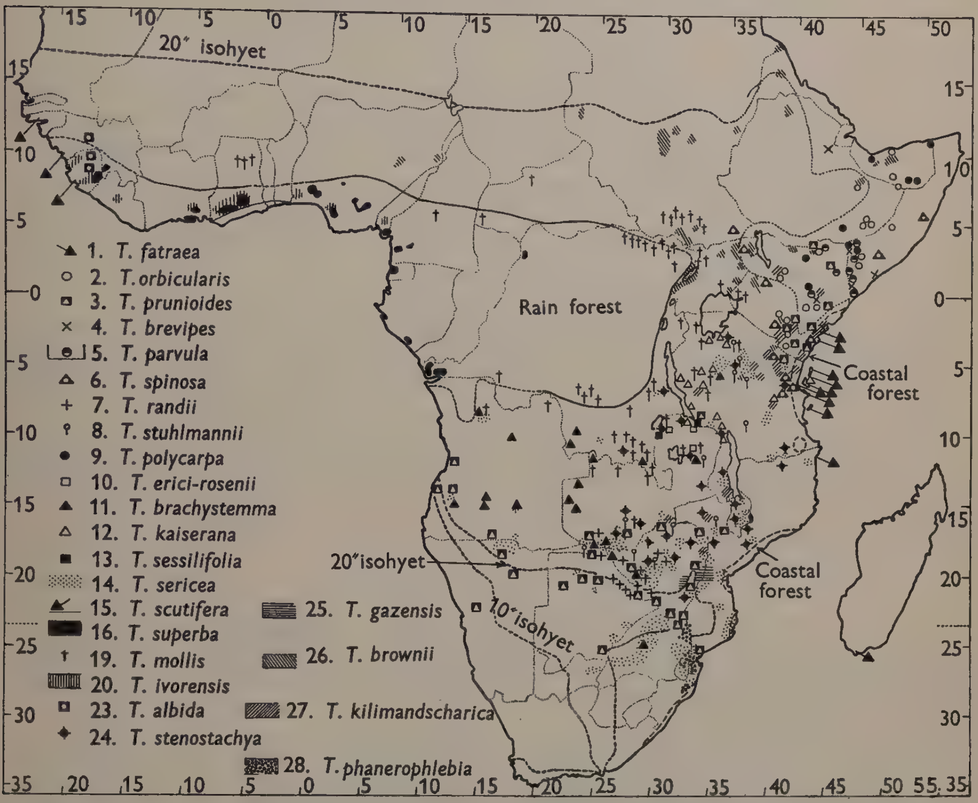

Fig. 29. Map showing localities of 24 species of *Terminalia* from which specimens have been examined. The distributions of *T. macroptera* (17), *T. laxiflora* (18), *T. glaucescens* (21) and *T. avicennioides* (22), which are widely distributed north of the Equator between the northern limit of rain forest and the 20-inch isohyet, are not shown.

T. chebula Retz (Sect. **Myrobalanus** (Gaertn.) Eichl.)

A native of India, where it is found in the northern parts from Kumaon to Bengal, and south to the Deccan; also in Ceylon and Burma. It is cultivated in various Malaysian gardens, and at Amani in Tanganyika.

The fruit is one of the commercial Myrobalans, and the black dye (with iron-clay) produces a good ink; when used with alum it produces a durable yellow dye. The timber is used for furniture.

T. arjuna (Roxb.) W. & A. (Sect. **Pentaptera** (Roxb.) Engl. & Diels)

A native of Ceylon and India, where it is distributed from the Deccan to the sub-Himalayan tracts of the north-western provinces. It is cultivated in various Malaysian gardens and also at Amani in Tanganyika.

The timber is known under the trade name of 'Arjun'. The bark is used for tanning.

VI. SUMMARY

The author has attempted a revision of all the African species of *Terminalia*. She has examined all of the type specimens, except those which were destroyed in Berlin during the recent war, those which are housed in the historic herbaria at Paris and Geneva, and those of two species collected by Italian botanists, which have not been located. She has studied approximately 1400 specimens, and this comprises the bulk of the material hitherto collected.

One hundred and fifteen specific names have been used in this genus in Tropical Africa; they have all been accounted for. Only twenty-eight species are fully accepted in this account; a key for their identification is provided; they are all fully described and each is illustrated by one plate of drawings. Synonymy is given in full, and reasons for that which is new are given. For each of the twenty-eight species a full bibliography, vernacular names, notes on variation and notes on distribution and ecology are given; a sufficient number of specimens to cover the geographical distribution and to illustrate the range of variation has been selected for citation.

Seven species which have been previously described and named are treated as being imperfectly known as the available material is scanty, and they only receive brief mention. All other names hitherto used in *Terminalia* in Africa are either treated as synonyms, or reasons are given as to why, at the present, they should not be used. Attention is drawn to a further five taxa, which may be new species, but have never been named and described; these are also treated as 'imperfectly known' species; the available material is insufficient to allow a more definite taxonomic judgement.

APPENDIX

Alphabetical index to all published names applied to African species.

T. adamauensis Engl. & Diels = **T. macroptera** Guill. & Perr., p. 864.
T. aemula Diels = **T. kilimandscharica** Engl., p. 897.
T. albida Scott Elliott, p. 887.
T. altissima A. Chev. = **T. superba** Engl. & Diels, p. 860.
T. angolensis O. Hoffm. = **T. sericea** Burch. ex DC., p. 853.
T. angolensis Welw. ex Ficalho = **T. sericea** Burch. ex DC., p. 853.
T. argyrophylla Engl. & Diels = **T. albida** Scott Elliot, p. 887.
T. avicennioides Guill. & Perr., p. 884.
T. bagamoyoana Engl., *Pflanzenw. Afr.* **3** (**2**), 724 (1921). No type-specimen cited.
T. balladellii Chiov., *Fl. Somala*, **2**, 207 (1932). Type-specimen (*Balladelli* 264) not seen. Italian Somaliland: Lungo il Lac Dera, Oltregiuba.
T. basilei Chiov., *Nuov. Giorn. Bot. Ital.* N.S., **36**, 364 (1929). Type-specimen (*Abruzzi* 336) not seen. Abyssinia: Dara.
T. baumannii Engl. & Diels = **T. glaucescens** Planch. ex Benth., p. 879.
T. baumii Engl. & Gilg. = **T. brachystemma** Welw. ex Hiern, p. 846.
T. benguellensis Welw. ex Hiern = **T. prunioides** Laws., p. 829.
T. bispinosa Schweinf. & Volkens ex Engl. & Diels, *Monogr.* **4**, 25 (1900). Type-specimen (*Ghika* s.n.) not seen.
T. brachystemma Welw. ex Hiern, p. 846.
T. brandisii Engl. ex Brandis, *Pflanzenfam.* **3** (**7**), 118 (1898), nom subnud.; no type specimen cited; almost certainly equals *T. fatraea* (Poir.) DC.
T. brevipes Pampan., p. 834.
T. brosigiana Engl. & Diels = **T. sericea** Burch. ex DC., p. 853.
T. brownii Fresen., p. 893.
T. bubu De Wild. & Ledoux = **T. sericea** Burch. ex DC., p. 853.
T. canescens Engl., *Pflanzenw. Ost Afr.*, C, 294 (1895); Engl. & Diels, *Monogr.* **4**, 18 (1900). Type-specimen (*Stuhlmann* 4285) not seen. Tanganyika; non *T. canescens* (DC.) Radlk. (1890).
T. chevalieri Diels = **T. laxiflora** Engl. & Diels, p. 868.

T. chrysomalla Gilg & Lederm. ex Engl. *Pflanzenw. Afr.* **3** (**2**), 722 (1921). No type-specimen cited.
T. claessensii De Wild. = **T. macroptera** Guill. & Perr., p. 864.
T. confertifolia Steud. ex A. Rich. = **T. brownii** Fresen., p. 893.
T. cycloptera R. Br. nom. nud. = **T. brownii** Fresen., p. 893.
T. dawei Rolfe = **T. macroptera** Guill. & Perr., p. 864.
T. dewevrei De Wild. & Th. Dur. = **T. mollis** Laws., p. 871.
T. dictyoneura Diels = **T. avicennioides** Guill. & Perr., p. 884.
T. dielsii Engl., *Pflanzenw. Afr.*, **3** (**2**), 720 (1921). No type-specimen cited.
T. dolichocarpa Engl. & Diels, *Monogr.* **4**, 35 (1900). Type-specimen (*Goetze* 458) not seen.
T. elliotii Engl. & Diels = **T. laxiflora** Engl. & Diels, p. 868.
T. emarginata Engl., *Pflanzenw. Afr.*, **3** (**2**), 723 (1921). No type-specimen cited.
T. erici-rosenii R.E. Fr., p. 845.
T. erythrophylla Burch., *Trav. S. Afr.* **1**, 400 = *Combretum erythrophyllum* (Burch.) Sond.
T. excelsior A. Chev. nom. nud. = **T. glaucescens** Planch. ex Benth., p. 879.
T. fatraea (Poir.) DC., p. 825.
T. fischeri Engl. = **T. sericea** Burch. ex DC., p. 853.
T. flava Engl. = **T. glaucescens** Planch. ex Benth., p. 879.
T. foetens Gilg ex Engl., *Pflanzenw. Afr.*, **3** (**2**), 724 (1921). No type-specimen cited.
T. gazensis Bak. f., p. 892.
T. glandulipetiolata De Wild. = **T. chebula** Retz, p. 903.
T. glandulosa De Wild. = **T. mollis** Laws., p. 871.
T. glaucescens Planch. ex Benth., p. 879.
T. hararensis Engl., *Bot. Jahrb.* **39**, 514 (1907). Type-specimen (*Ellenbeck* 1191) not seen. Somaliland.
T. hecistocarpa Engl. & Diels, *Bot. Jahrb.* **39**, 514 (1907). Type-specimen (*Ellenbeck* 1982) not seen. ? Abyssinia.
T. hemignosta Steud. ex A. Rich. pro syn. sub *brownii*; ex Delile in Ferret & Galin., descr. = **T. brownii** Fresen., p. 893.
T. hildebrandtii Engl. = **T. kilimandscharica** Engl., p. 897.
T. holstii Engl. = **T. prunioides** Laws., p. 829.
T. holtzii Diels, *Engl. Bot. Jahrb.* **39**, 513 (1907). Type-specimen (*Holtz* 1637) not seen. Tanganyika.
T. ivorensis A.Chev., p. 876.
T. kaiserana F. Hoffm., p. 849.
T. kelleri Engl. & Diels = **T. polycarpa** Engl. & Diels, p. 843.
T. kerstingii Engl. = **T. mollis** Laws., p. 871.
T. kilmandscharica Engl., p. 897.
T. laeteviridis Gilg & Lederm. ex Engl., *Pflanzenw. Afr.* **3** (**2**), 720 (1921). No type-specimen cited.
T. laxiflora Engl. & Diels, p. 868.
T. lecardii Engl. & Diels = **T. avicennioides** Guill. & Perr., p. 884.
T. longipes Engl. = **T. glaucescens** Planch. ex Benth., p. 879.
T. macroptera Guill. & Perr., p. 864.
T. mangela De Wild.—Imperfectly known species, see p. 891.
T. mildbraedii Gilg ex Mildbr., *Dtsch. Z. Afr. Exped.* 1907–8, **2**, 581 (1913). Type-specimen (*Mildbraed* 307) not seen. Bukoba Bezirk: Lager Nyavatura am Kagera.
T. mollis Laws., p. 871.
T. morogorensis Engl., *Pflanzenw. Afr.*, **3** (**2**), 720 (1921). No type-specimen cited.
T. mpapwensis Engl., *Pflanzenw. Afr.* **3** (**2**), 722 (1921). No type-specimen cited.
T. nyassensis Engl. = **T. sericea** Burch. ex DC., p. 853.
T. obovata Sim, *For. Fl. Port. E. Afr.*, p. 65, t. 64B (1909), non *T. obovata* Cambess. (1829). Type-specimen (*Sim* 5672) not seen.
T. omahekensis Dinter, *Fedde. Rep. Beih.* **53**, 119 (1928), nom. nud. in obs.
T. orbicularis Engl. & Diels, p. 827.
T. parvula Pampan, p. 835.
T. passargei Engl. = **T. glaucescens** Planch. ex Benth., p. 879.
T. petersii Engl. = **T. prunioides** Laws., p. 829.

T. phanerophlebia Engl. & Diels, p. 900.
T. poliotricha Diels, *Engl. Bot. Jahrb.* **54**, 342 (1917). Type-specimen (*Holtz* in Herb. Forst. Daressalam n. 3144) not seen. Tanganyika: Mlalital, West Ulugurus.
T. polycarpa Engl. & Diels, p. 843.
T. porphyrocarpa Schinz = **T. prunioides** Laws., p. 829.
T. praecox Engl. & Diels = **T. orbicularis** Engl. & Diels, p. 827.
T. prunioides Laws., p. 829.
T. randii Bak. f., p. 839.
T. rautanenii Schinz = **T. prunioides** Laws., p. 829.
T. repanda A. Chev. nom. nud. = **T. laxiflora** Engl. & Diels, p. 868.
T. reticulata Engl. non Roth. = **T. mollis** Laws., p. 871.
T. rhodesica R. E. Fr. = **T. stenostachya** Engl. & Diels, p. 888.
T. riparia Engl. & Diels, *Monogr.* **4**, 35 (1900). Type-specimen (*Goetze* 457) not seen.
T. robecchii Chiov. = imperfectly known species, see p. 845.
T. roseogrisea Gilg & Lederm. ex Engl., *Pflanzenw. Afr.* **3** (2), 720 (1921). No type-specimen cited.
T. ruspolii Engl. & Diels = **T. orbicularis** Engl. & Diels. p. 827.
T. salicifolia Schweinf. Imperfectly known species, see p. 870.
T. sambesiaca Engl. & Diels = **T. kilimandscharica** Engl., p. 897.
T. schimperana Hochst. ex Engl. & Diels = **T. glaucescens** Planch. ex Benth., p. 879.
T. schweinfurthii Engl. & Diels = **T. laxiflora** Engl. & Diels, p. 868.
T. scutifera Planch. ex Laws., p. 858.
T. semlikiensis De Wild. = **T. brownii** Fresen., p. 893.
T. sericea Burch. ex DC. (1828) non Cambess. (1829), p. 853.
T. sessilifolia R.E. Fr., p. 851.
T. silozensis Gibbs. Imperfectly known species, see p. 849.
T. sokodensis Engl. = **T. laxiflora** Engl. & Diels, p. 868.
T. somalensis Engl. & Diels. Imperfectly known species, see p. 845.
T. spekei Rolfe = **T. mollis** Laws., p. 871.
T. spinosa Engl., p. 836.
T. splendida Engl. & Diels, *Monogr.* **4**, 17, t. 7 C (1900). Type-specimens (*Fischer* s.n., *Fischer* 256) not seen.
T. stenostachya Engl. & Diels, p. 888.
T. stuhlmannii Engl., p. 840.
T. suberosa A. Chev. nom. nud. = **T. macroptera** Guill. & Perr., p. 864.
T. suberosa R. E. Fries = **T. mollis** Laws., p. 871.
T. superba Engl. & Diels, p. 860.
T. tessmannii J. D. Kennedy, *For. Fl. S. Nig.*, p. 46, nom. nud. No type-specimen cited.
T. thomasii Engl. & Diels, *Monogr.*, **4**, 18, t. 8B (1900). Type-specimen (*Thomas* 71) not seen. Somaliland.
T. togoensis Engl. & Diels = **T. glaucescens** Planch. ex Benth., p. 879.
T. torulosa F. Hoffm. = **T. mollis** Laws., p. 871.
T. trichopoda Diels. Imperfectly known species, see p. 858.
T. tristis Gilg & Lederm. ex Engl., *Pflanzenw. Afr.*, **3** (2), 720 (1921). No type-specimen cited.
T. velutina Rolfe = **T. glaucescens** Planch. ex Benth., p. 879.
T. verdickii De Wild. & Ledoux. Imperfectly known species, see p. 892.

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